THE DENTITION OF THE TITANOSUCHIAN DINOCEPHALIANS

By

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(With 1 plate and 41 figures in the text)

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Introduction

In the South African Dinocephalia the teeth are but poorly known. The inadequate accounts hitherto given by the authors, who have studied this sub-order, are chiefly due to the nature of the preservation of the studied material and the rather rough methods of preparation hitherto employed.

Many specimens are recovered only when already naturally weathered out of the entombing rock and lying exposed on the eroded surface of the rocks of the *Tapinocephalus* zone as broken-up pieces weathered to various degrees. In the cranial material thus collected the crowns of the teeth are seldom well preserved, but exceptionally such material has yielded isolated well-preserved crowns. Such is the case in specimens which when petrified had full sets of teeth, but it is evident that a large number of skulls had on death lain exposed before entombment and during this time many of the teeth had often either fallen out of their sockets or had their crowns damaged or wholly broken off. This is evident from the fact that in many cases we find empty alveoli filled by matrix and by the fact that loose-lying teeth occur lying near parts of the skull or even unassociated with any other skeletal material, the harder dental substance being preserved and the less hard bone being lost. During thirty-two years of collecting in the *Tapinocephalus* zone I have found that the whole

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teeth—crown plus root—fall out of the alveoli before petrifaction more frequently in the Tapinocephalia than in the other three infra-orders; and in the Titanosuchia the crowns are broken off at the level of the alveolar border either before petrifaction or during the later weathering more frequently than in the other infra-orders. I believe this to be due to the difference in implantation and the mode of replacement of the teeth in these infra-orders.

When crowns are preserved *in situ* the intractable matrix makes good preparation difficult with the older hammer-and-chisel technique employed. Improved newer mechanical methods—vibro-needles and sectioning with rotating diamond-studded saws—and chemical solution now give better results in suitable specimens. If available, radiography would be a further improvement.

General

The dentition of the sub-order Dinocephalia (Anteosauria, Titanosuchia, Tapinocephalia and Styracocephalia) can be readily distinguished from those obtaining in all the other contemporary sub-orders of the order Therapsida by the following distinctive character:

In occlusion the upper and lower incisors intermesh, whereas in all the other contemporary therapsids with incisors (thus excluding the anomodonts) the upper incisors pass labially of the lower incisors. This distinctive intermeshing is developed further in the Titanosuchia, where the lower canine passes in front of the upper canine to intermesh between the last upper incisor and the upper canine (fig. 1). This process is carried still further in the Tapinocephalia and the Styracocephalia where the whole battery of teeth intermesh.

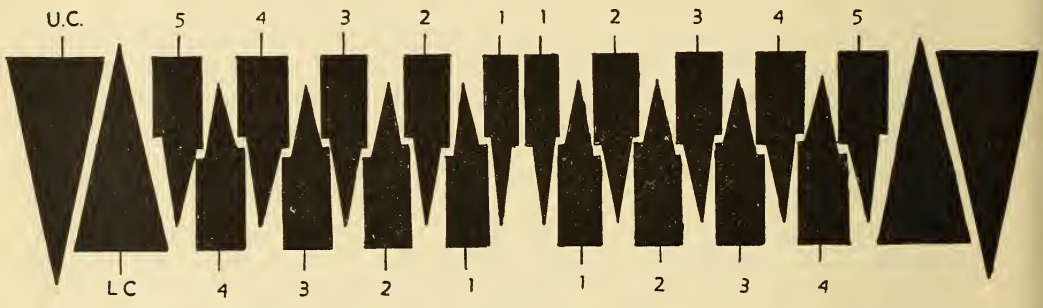


Fig. 1. A diagram to illustrate the intermeshing of the incisors and canines in the Titanosuchia.

Abbreviations used in this and subsequent figures:

1–5 = functional incisors. 1′–5′ = first replacing incisors. 1″–5″ = second replacing incisors. 1°–5° = predecessors to the functional incisors. An = angular. Ar = articular. C = canine. C^1 = replacing canine. Cor = coronoid. D = dentary. F = lingual flange of the dentary. F. Pt. = fossa for the quadrate ramus of the pterygoid. G = groove labial to the flange of the dentary. H = heel of the tooth. I.C. = inner condyle. L.C. = lower canine. M = maxilla. m = maxillary tooth. m^1 = replacing maxillary tooth. N = nasal. O.C. = outer condyle. Pa = prearticular. Pal = palatine. PC = postcanine. PC^1 = replacing postcanine. PC^1a = alveolus for replacing postcanine. Pm = premaxilla. Proc = processus musculus pterygoidus posterius. Pt = pterygoid. Q = quadrate. Q.F. = foramen quadrati. QRPt = quadrate ramus of the pterygoid. R = root of the tooth. Sa = surangular. Sm = septomaxilla. Sp = splenial. St = stapedial recess on the quadrate. T = talon of the tooth. U.C.. = upper canine. V = vomer.

This intermeshing of the teeth is, I believe, a character of sufficient importance, when taken in conjunction with other evidence available from the rest of the dinocephalian skeleton, to validate the old conception of grouping the four infra-orders together in one sub-order—Dinocephalia, and to show that the newer attempts in classification which are intended to refute this close consanguinity are ill-advised and contrary to the facts.

Although the four infra-orders of the Dinocephalia are linked together by this common character of intermeshing, there are certain dental features (together with other skeletal characters) distinctive of each infra-order, but all derivable from one common ancestral condition.

The dentition in the Titanosuchia can be readily distinguished from that of the Tapinocephalia and Styracocephalia by the presence of large specialized canines in both upper and lower jaws; from that in the Anteosauria, which also have large specialized canines, by the fact that in the Titanosuchia the lower canine is directed both outwards and forwards to intermesh between the upper canine and the fifth upper incisor, whereas in the Anteosauria the lower canine is directed upwards to lie inside the upper canine with its point housed in a special recess in the maxilla.

The infra-order Titanosuchia has, on skeletal characters other than those shown by the dentition, been subdivided into the three families Titanosuchidae, Jonkeriidae and Dinartamidae.

The dental material at my disposal has not enabled me to recognize differences in the dentition to substantiate this subdivision into families—a subdivision which is undoubtedly valid for the former two families. The family Dinartamidae founded on a single very poor specimen is of doubtful validity.

Material

This report on the dentition of the Titanosuchia is based mostly on the material in the collection of the South African Museum. This consists of 37 specimens, from isolated localities situated over the whole of the western fossiliferous part of the *Tapinocephalus* zone, in which adequate evidence of the dentition is preserved. Of these 37 specimens, 1 is from an unknown collector, 1 collected by Cloete, 1 by Cairncross, 1 by Hugo, 3 by Whaits, 3 by Haughton and the other 27 by the author.

Although the majority of these specimens are poorly preserved, the total of the determinable features gives us a fairly complete picture of the nature of the dentition in the infra-order as a whole. The available facts are, however, insufficient as reliable characters employable for taxonomic purposes within the group. Such characters as have been used by previous authors for the establishment of genera and species do not at present appear to be sufficiently distinctive or constant and such classification must at the present stage be considered of doubtful validity.

Descriptive

General

Before giving an account of the individual specimens, in an attempted taxonomic order, the general features of the dentition of the infra-order as a whole follows.

In the Titanosuchia a full and mature set of teeth gives the formula:

$$i\,\tfrac{5}{4},\quad c\,\tfrac{1}{1},\quad pc\,\tfrac{19}{18-21}.$$

Where previous authors have given different formulae for their specimens and in the specimens at my disposal, which give a different count, these differences should at present, without further confirmatory evidence, not be attributed to any taxonomic distinction. That the different genera and species

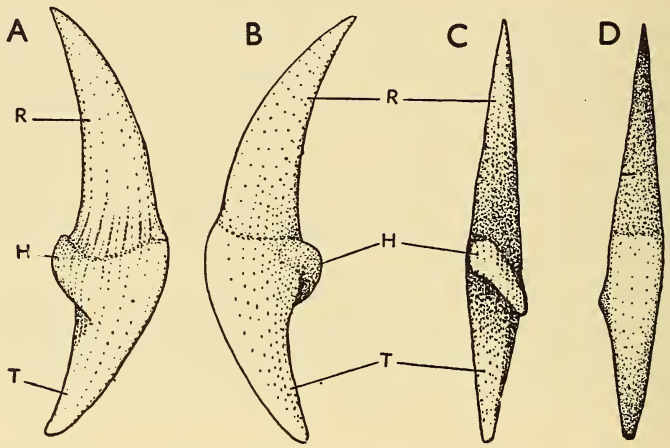


Fig. 2. *Jonkeria*. The left second upper incisor S.A.M. E. $\times\frac{1}{2}$.
A = anterior or inner view.
B = posterior or outer view.
C = lingual view.
D = labial view.

may have had different numbers of post-canines cannot, of course, be discounted; but in the light of our present knowledge such differences should rather be considered to be due to imperfect observation, imperfect preservation, age of the animal, or to the stage which the replacement of the teeth happens to have reached in each individual jaw. Noted differences in the left and right sides of the jaws of the same beast bear this out.

The Incisors

Both the upper and lower incisors have the structure which has been called 'dinocephalian' by various authors. What these authors really mean is that the incisors have the general structure of the teeth of the Tapinocephalia (especially the Russian *Deuterosaurus* and *Ulemosaurus*). Later in this paper it will be shown

that the titanosuchian incisor can be readily (figs. 2 and 3) distinguished from the tapinocephalian teeth.

Essentially the distinctive structure of these teeth is the development in the crown of a piercing point separated from a cutting and/or crushing surface. Each tooth consists of a strong, long, curved, conical root; oval in section, and a nearly equally long, curved, claw-like point or talon with a convex labial face and a flattened lingual face with longitudinal striae and fairly flat sides. At the

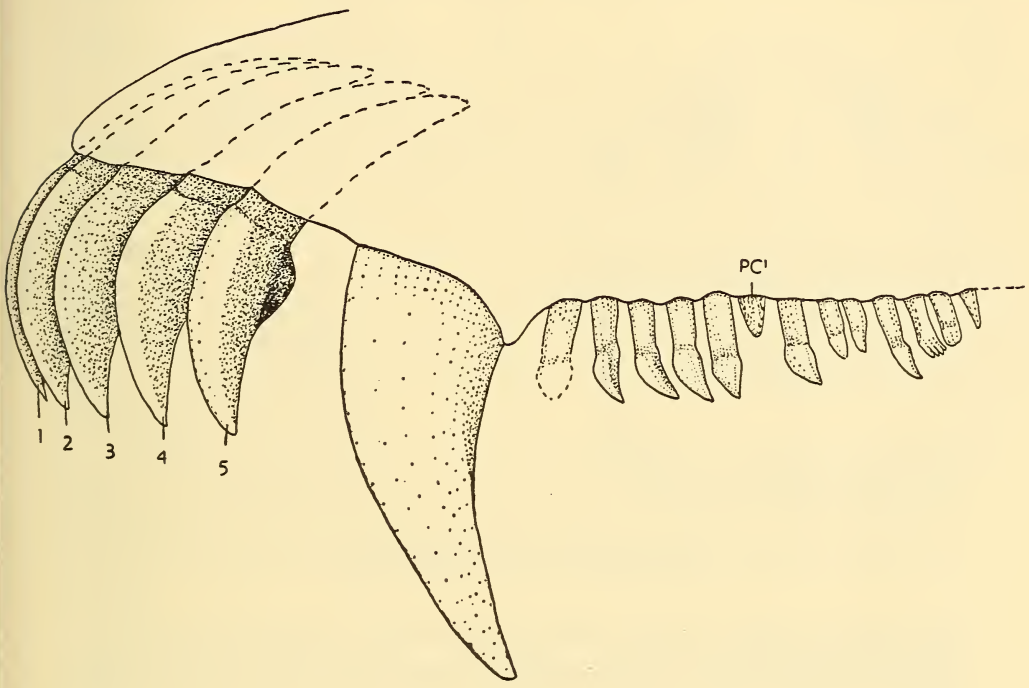


FIG. 3. *Jonkeria*. Lateral view of the upper jaw teeth. S.A.M. E. $\times \frac{1}{2}$. Partly restored.

junction of crown and root the crown has on its lingual or inner face an oblique step, heel or cingulum. This heel forms an oblique ledge with its outer part higher than its inner part in the upper incisors and its outer part lower and its inner part higher in the lower incisors. In the unworn tooth the lingual edge of this heel forms a fairly sharp ridge with coarse serrations; after some wear the edge loses its serrations and the sharp edge becomes rounded; when greatly worn the edge is lost and the whole ledge acquires a flat face. Concomitant with this wear of the heel the talon is also worn away lingually to become more and more slender and thereby increasing the size of the crushing flat face of the heel.

There are certain differences between the five upper *inter se* and between the four lower incisors (fig. 4).

The first pair of upper incisors is more lightly built than all the others; this lightness is mainly due to the fact that the teeth are compressed from side to side, lying close together and, in occlusion, passing their talons in between the pair of lower incisors. The fifth upper incisor has the rear face of the talon modified to receive the lower canine with which it intermeshes. In the lower jaw the fourth incisor is somewhat weaker than the anterior ones. Other differences

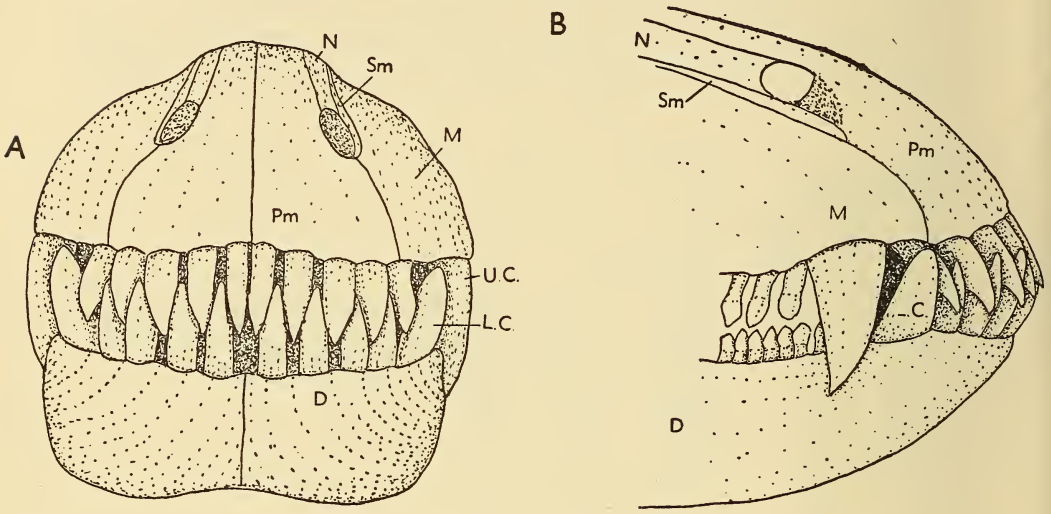


Fig. 4. *Jonkeria*. S.A.M. 9162. ×¼.
A = anterior view. B = lateral view.

between the incisors can best be attributed to age or wear, but with more material available some of these differences may prove to be of taxonomic value.

The length of the incisor series varies in length: upper 73–106 mm. and lower 68–94 mm., but the variation between the two sides of the jaw is such that these measurements have a doubtful taxonomic value.

In occlusion the incisors of the two jaws intermesh (fig. 1) as follows:

The talons of the upper No. 1 pair lie in between the talons of the lower No. 1 pair.

Upper No. 2 lies between lower Nos. 1 and 2.
Upper No. 3 lies between lower Nos. 2 and 3.
Upper No. 4 lies between lower Nos. 3 and 4.
Upper No. 5 lies between lower No. 4 and the lower canine.

The outer half of the heel of upper No. 1, abuts against the inner half of the heel of lower No. 1; the heel of upper No. 2 has its inner half abutting

against the outer half of the heel of lower No. 1 and its outer half against the inner half of lower No. 2; similarly upper No. 3 abuts against the halves of lower 2 and 3; upper No. 4 abuts against the halves of lower 3 and 4; upper No. 5 abuts against the halves of lower 4 and the inner face of the lower canine. The inner face of the lower canine shows in some specimens an oval worn face where attrition by the upper No. 5 incisor takes place.

In both upper and lower jaws the incisors do not stand vertically in the jaws but are directed forwards so that in occlusion the tips of the talons protrude anteriorly.

The Canines

Each maxilla and dentale bears a single robust canine (figs. 3 and 4).

The upper canine has a large conical crown which curves moderately to strongly backwards and is moderately flattened from side to side to present a greater or lesser oval in cross section, its posterior face is rounded with no sharp edge or serrations. The root is large and long and its presence causes the maxilla to bulge both externally as well as internally; internally the root opens on to the inner face of the maxilla, where the large pulp cavity remains open for the passage of nerve and nutrient vessels (fig. 31).

Where it leaves the jaw the canine diameters vary from 35 to 50 mm. antero-posteriorly and from 21 to 36 mm. from side to side. The crown length varies from 60 to 110 mm.

Between the last upper incisor and the canine there is a moderate diastema ±20 mm. which allows the lower canine to pass between these two teeth. In occlusion the upper canine passes behind the lower canine and fits in a hollow in the outer face of the dentale. In place of the lower canine lying lingually of the upper canine in occlusion there are here situated the first 4–5 lower postcanines.

The lower canine is smaller than the upper, shorter and less pointed and curved, with its blunted point directed outwards to pass in between the upper canine and the 5th upper incisor and to pass externally of the edge of the upper jaw. Its intero-anterior face frequently shows an attritional face where the last upper incisor wears against it. The outwardly directed lower canine has by Broom been considered a distinctive character of *Scapanodon*, but it is a feature common to all the known Titanosuchia, which in this character differ from all other contemporary Therapsida.

The Postcanines

The postcanines (fig. 5) form a long series in both jaws. The spacing is close and, except where replacement is taking place, regular. They differ from both the incisors and canines in that the teeth of the upper and lower jaws do not intermesh. In occlusion the lower set lies lingually of the upper set, as is normal, in the contemporary therapsids. The upper set is implanted close to the outer edge of the maxilla, whereas the lower set lies close to the inner edge

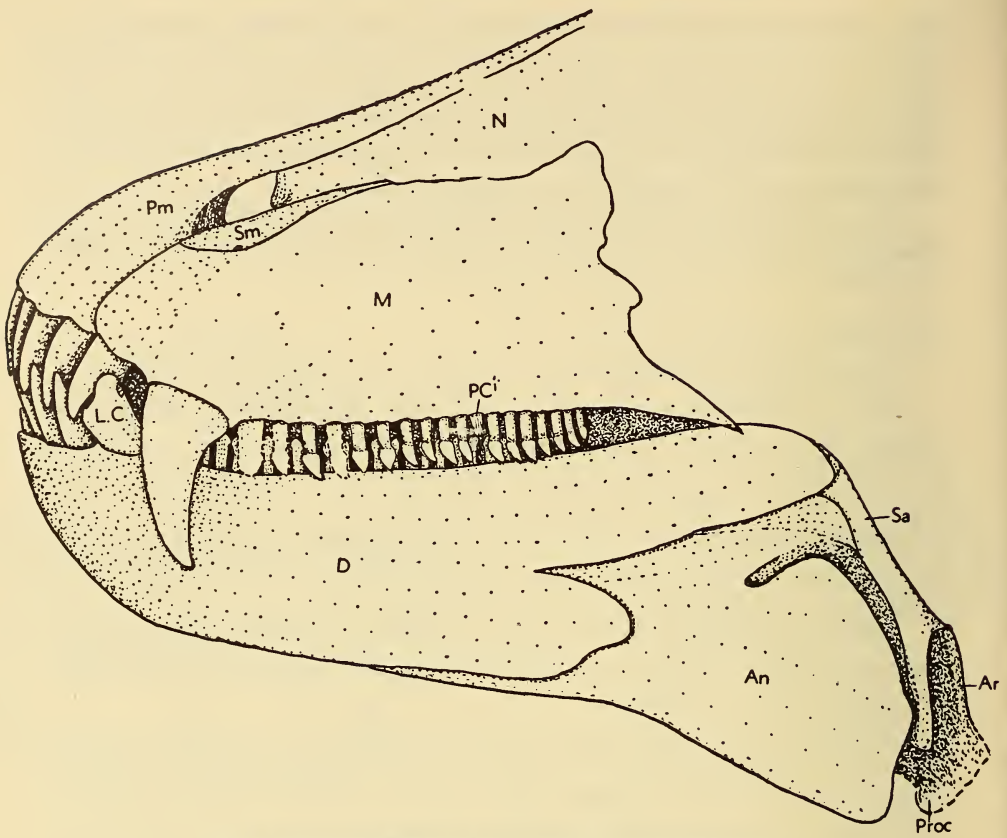


FIG. 5. *Jonkeria truculenta*. S.A.M. 12030. ×½. Lateral view.

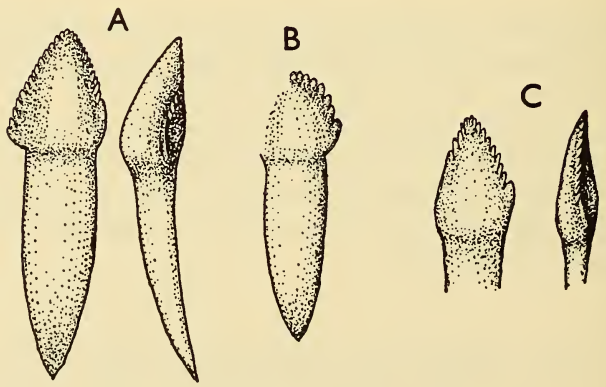


FIG. 6. *Parascapanodon*. S.A.M. 12213 ×½.

A = right upper postcanine in labial and posterior view.
B = a postcanine in labial view.
C = the 11th right lower postcanine in labial and posterior view.

of the dentale, with on their outside, a groove for the reception of the upper set. The upper postcanines are somewhat larger than the lower ones, but built on essentially the same plan. In both jaws the crowns lie obliquely to the long axis at an angle of about 40°, with the anterior edge directed inwards and the posterior edge outwards. The first postcanine in both upper and lower jaws is directed somewhat anteriorly and is usually the largest postcanine, the next four to five are of the same size, and the rest gradually decrease in size backwards. The postcanines in both jaws follow on their respective canines without a diastema. As the lower canine passes anteriorly of the upper canine, and the length of upper and lower series being approximately equal, it follows that the last 4–5 upper postcanines have no lower antagonists. Furthermore in occlusion the first 4–5 lower postcanines lie lingually of the upper canine.

Each postcanine (fig. 6) consists of a long root more or less oval in section, with a spatulate crown roughly triangular in outline; the outer face is moderately convex and the inner face flat to slightly concave. Both inner and outer faces carry fairly coarse striae, which in unworn teeth extend to the edge which thus becomes serrate.

In my specimens the length of the upper series varies from 169 to 188 mm. and the lower set from 165 to 210 mm.

The full set of postcanines numbers 19–21; in those specimens with a shorter set and a lesser number of teeth it would be reasonable to assume juvenility, additional teeth being added posteriorly with increasing age.

Tooth Replacement

In nearly every specimen replacement of teeth can be seen (figs. 7 and 8). Evidence of this is, first, irregularity in the series, the presence of empty alveoli, and, lastly, the presence of crowns in the process of eruption. Replacement occurs in incisors, canines and postcanines, but due to the great mass to be replaced replacement is less frequently seen in the large canines.

There is evidence of at least two sets of canines and postcanines and of at least three sets of incisors. Replacement may thus be a continuous process—there being no positive evidence of it ceasing.

In all the teeth the immediate replacing tooth erupts lingually of its predecessor and is thus a younger member of the same tooth family. In the Titanosuchia functional distichism thus no longer occurs.

Since in each tooth, generation follows generation independently, at any given time the functional teeth are, except initially, never all of the same age or generation. This is specially noticeable in the incisors, where in almost every set of functional teeth very distinct stages of development and subsequent wear can be seen. In many cases, from the stage of wear of the functional incisors, the order of replacement can be deduced and this can then be verified by noting the degree of development of their respective replacing teeth.

Replacement of the Incisors

In the premaxilla (fig. 7) a cavity develops in the bone lingually of the alveolus which houses each functional incisor. This cavity houses the germ from which the replacing incisor develops. By the time the replacing crown reaches a certain stage of development the inner or lingual wall of this cavity develops, by resorption of the bony tissue, a perforation. This opening enlarges to form a long oval fenestra and through this fenestra the crown of the replacing tooth

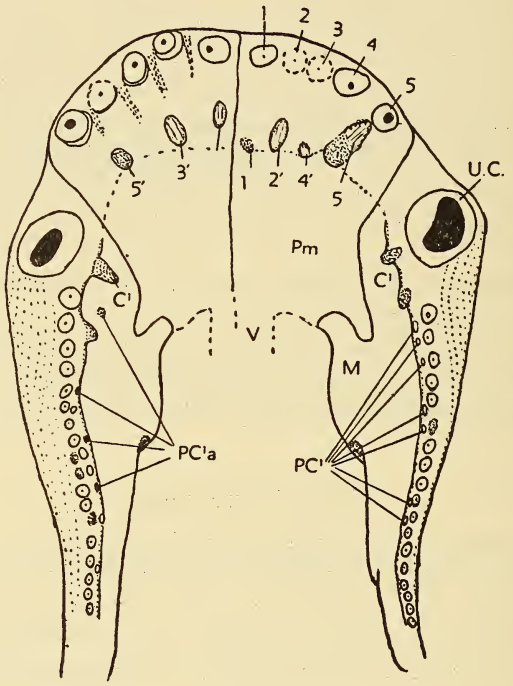


FIG. 7. *Jonkeria boonstrai*. S.A.M. 9079 ×¼.
Ventral view of upper jaws.

emerges. As the replacing tooth continues its growth it moves labially into the lingual wall of the alveolus of the functional tooth which is gradually reabsorbed, until the new alveolus coalesces with the old alveolus. The old tooth has concomitantly suffered resorption and as it disappears the new tooth takes over its alveolus. In the meantime the fenestra through which the replacing crown can first be seen has closed up from above downwards so that the new tooth when arriving in the old alveolus has its own lingual alveolar wall. The talon of the young tooth, when just emerging, is flattened antero-posteriorly, roughly triangular in outline with its inner face coarsely striate and since these striae extend to the edges these are serrate.

Noting the degree to which each replacing incisor crown has developed, I have tried to determine if there is a regular order in the replacement. (This can be controlled by noting the degree of wear in the crowns of the functional incisors.) But as could be expected this was not possible.

In the dentary (fig. 8) the eruption of the replacing incisors appears to follow a different course than noted in the upper incisors. This is due to the fact that in the dentary there lies lingually to the erupting incisors a flange of bone with a free upper edge, which thus forms a groove labially and at first sight it appears as if the replacing incisors emerge from this groove.

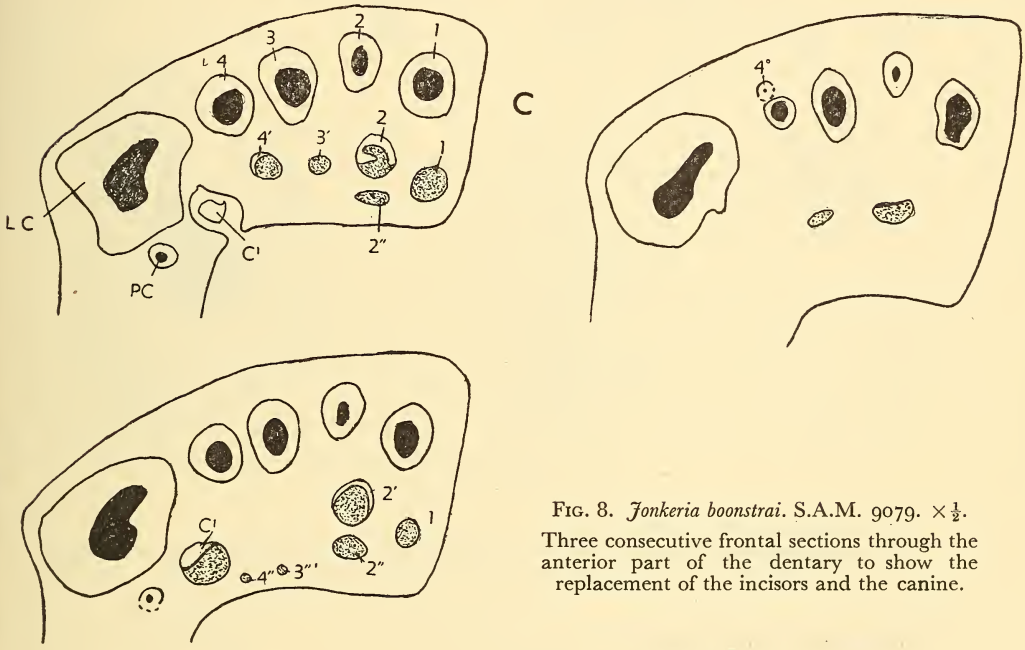


FIG. 8. *Jonkeria boonstrai*. S.A.M. 9079. ×½.
Three consecutive frontal sections through the anterior part of the dentary to show the replacement of the incisors and the canine.

When seen in section (fig. 9), however, it is clear that the replacing teeth develop in cavities in the solid dentary labially of this groove. The mode of development is thus similar to that of the upper incisors, viz. lingually of each alveolus housing a functioning incisor a cavity is formed in which the tooth germ develops and the further course of development parallels that already described for the upper incisors.

Replacement of Canines

Little is known of the replacement of the canines (figs. 7 and 8). In the upper jaw there is frequently a small hollow in the lingual wall of the maxilla just above the inner alveolar edge of the functional canine. That this hollow indicates the point of eruption of the replacing canine as do the fenestrae lying

lingually of the incisors is proved by the one case (S.A.M. 11884) where on both sides it houses the tip of the replacing canine. In two cases we have an empty canine alveolus, but in neither can a replacing tooth be determined with certainty.

In the lower jaw a hollow lying lingually of the posterior end of the inner free-edged flange of the dentary is frequently present and this in four cases houses a small tip of the replacing canine.

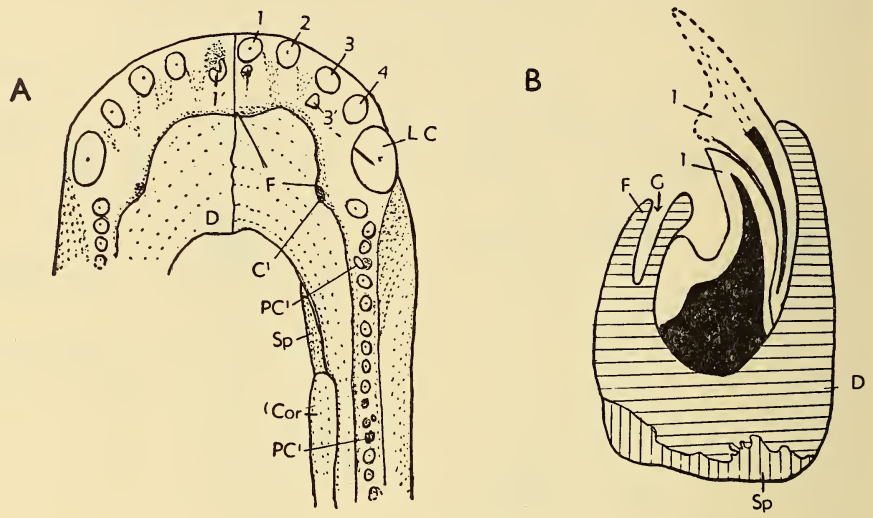


FIG. 9. *Jonkeria*. S.A.M. 9161.

A = dorsal view of mandible $\times \frac{1}{4}$.
B = fracture through the jaw at the level of the first right incisor showing the dental flange (F) with its free upper border and the groove (G) lying labially. $\times \frac{1}{2}$.

Replacement of the Postcanines

In both upper and lower jaws the emerging cusps of replacing teeth can frequently be seen, each lying lingually of either a functional tooth of the same family or of an alveolus from which its predecessor has disappeared (fig. 7). The replacing crown-tips appear on the alveolar border without the development of a fenestra in the lingual wall of the jaws as is the case in both incisors and canines. Some, at least, of the replacing postcanines arise in separate alveoli lying lingually of those of the functional teeth and these alveoli coalesce on the loss of the functioning tooth. The erupting teeth appear as striate, serrate tips triangular in outline.

Usually each series of postcanines has only a few replacing tips showing, but in a few specimens a larger number—up to 9—have erupted at more or less the same time. At the most 3 adjacent teeth have been seen erupting together, but mostly the erupting teeth appear at irregular intervals.

Descriptive

(Specimens Taxonomically)

Titanosuchidae

Genera Archaeosuchus and Scapanodon

The dental material which constitutes the types of these genera is so poorly preserved that no useful purpose will be served by attempting to add to Broom's descriptions.

Genus Parascapanodon

Parascapanodon avifontis

(Fig. 10)

S.A.M. 9127. Type. Voëlfontein, P.A. Collected Boonstra 1929.

This specimen consists of parts of a skull including parts of the upper and lower jaws together with good bones of the postcranial skeleton.

Apart from some roots of the upper incisors there is an incomplete right mandibular ramus showing the roots of most of the teeth.

Of the incisors only the root of the fourth is present. The canine root is oval in section (diams. 28 and 36 mm.) and the lingual wall of the alveolus shows an opening for the replacing canine. The set of postcanines consisted of 21 teeth of which the first is much larger than the rest. Nos. 8, 10, 12 and 15 are replacing teeth lying lingual of alveoli from which the former set has fallen out.

The length of the postcanine series is 180 mm.

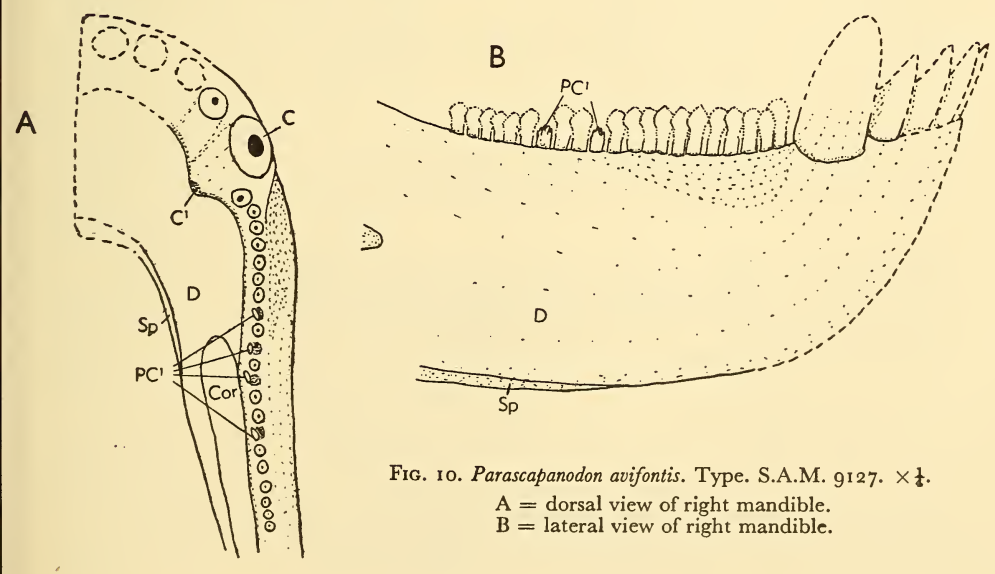


Fig. 10. *Parascapanodon avifontis*. Type. S.A.M. 9127. ×½.
A = dorsal view of right mandible.
B = lateral view of right mandible.

Parascapanodon sp.

S.A.M. 12213. Kroonplaas, B.W. Collected Boonstra 1959.

Under this number there are parts of at least three individuals found together. Besides some skull pieces, a number of isolated loose-lying teeth and a fibula, are preserved:

A (fig. 11). A fairly good anterior two-thirds of a mandibular arch in which crowns of the teeth are preserved in a fair condition. The dental formula is $\frac{\text{i 4, c 1, pc 19}}{}$.

Incisors

On the left side the crowns are broken off just below the heel. Lingually of No. 2 lies the erupted crown of its replacement. It lies in the groove just

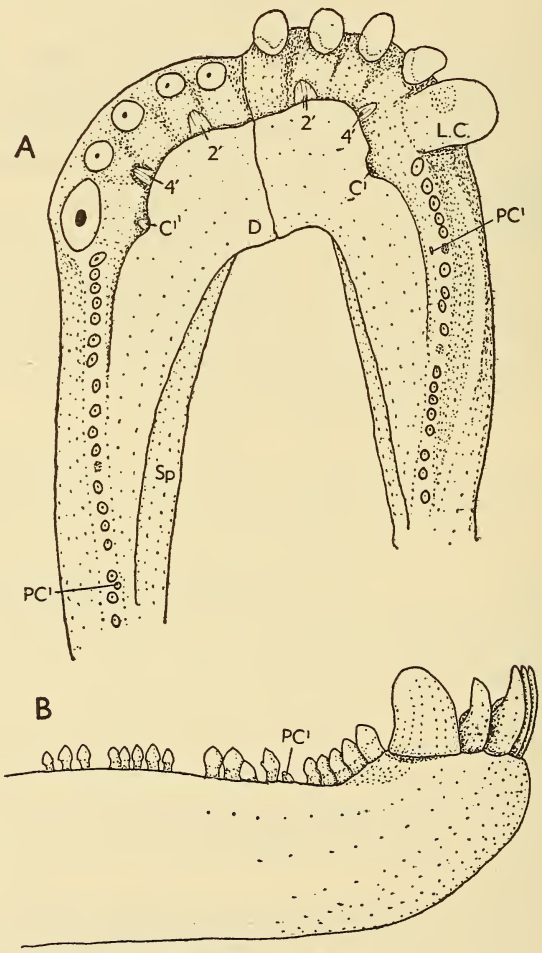


FIG. 11. *Parascapanodon* sp. S.A.M. 12213 A. $\times\frac{1}{4}$.
A = dorsal view of mandibles.
B = lateral view of the right mandible.

anterior to the flange of the dentary and against the lingual alveolar wall of the functioning tooth. Its inner face is striate. Lingually of No. 4 a pocket in the alveolar wall contains the crown of its replacement.

In the right dentary the four incisors are well preserved—only the tips of the talons being lost. The heels of all four are very well preserved, and are very little worn so that the lingual edge still forms a raised edge with a hollow between this edge and the posterior face of the talon; and in No. 4 the posterior surface of the talon still shows fairly coarse striae.

Lingual of Nos. 2 and 4 replacing crowns are present in their respective pockets.

The fact that replacing crowns are already showing, while the functioning crowns are still little worn, indicates that considerable time may elapse before the actual replacement takes place.

Canines

The left canine is broken off at the base of the crown, which is here oval in section with diameters 39 and 28 mm. Of the right canine the tip of the crown is lost. It is a moderately sized tooth (basal diameters 38×28 mm.) directed much outwards. On its antero-internal face there is an oblique groove in which the 5th upper incisor fitted in occlusion.

Lingual to both canines there is a notch in the flange of the dentary and a pocket in the internal alveolar wall for the emergence of the replacing canines.

The Postcanines

On the left dentary only a few crowns are preserved—the rest being broken off below the spatulate crown. The presence of 19 postcanines can be determined occupying 197 mm.—No. 12 is represented by an empty alveolus and there is a replacing crown lying postero-lingual to No. 17. No. 1 is large (diams. 9×7 mm.), whereas No. 5 is only 7×6 mm. and the others approximately of this size.

In the right dentary the crowns of the postcanines are better preserved. The original presence of 19 teeth occupying 188 mm. can be determined. No. 6 and No. 11 are represented by empty alveoli and lingual of alveolus 6 is a replacing crown.

The crown of the 1st postcanine is widely spatulate, with a convex outer and a flattened internal face; the edges are sharp and coarsely serrate. This, as also the other postcanines, have their spatulate crowns lying obliquely to the long axis of the skull, with the anterior edge lingually and the outer labially directed. In lateral view they thus overlap where closely spaced.

The other postcanines are very similar to No. 1, except that their crowns are smaller and the spatula more sharply triangular in outline. There is a gradual decrease in size posteriorly.

The postcanines lie on the inner part of the upper dentary edge; external to the tooth row there is a longitudinal groove for the reception of the upper postcanines.

B (fig. 12). A mandibular arch in somewhat better condition than A.

In the left dentary the four incisors and the canine have the major part of their crowns preserved; of the postcanines only the first five and last two are preserved and they occupied 194 mm.

In the right dentary most of the crowns of the four incisors, canines and the original 18 postcanines are preserved. The postcanine series measures 199 mm. and lingual of No. 7 there is a replacing crown and No. 13 is represented by an empty alveolus.

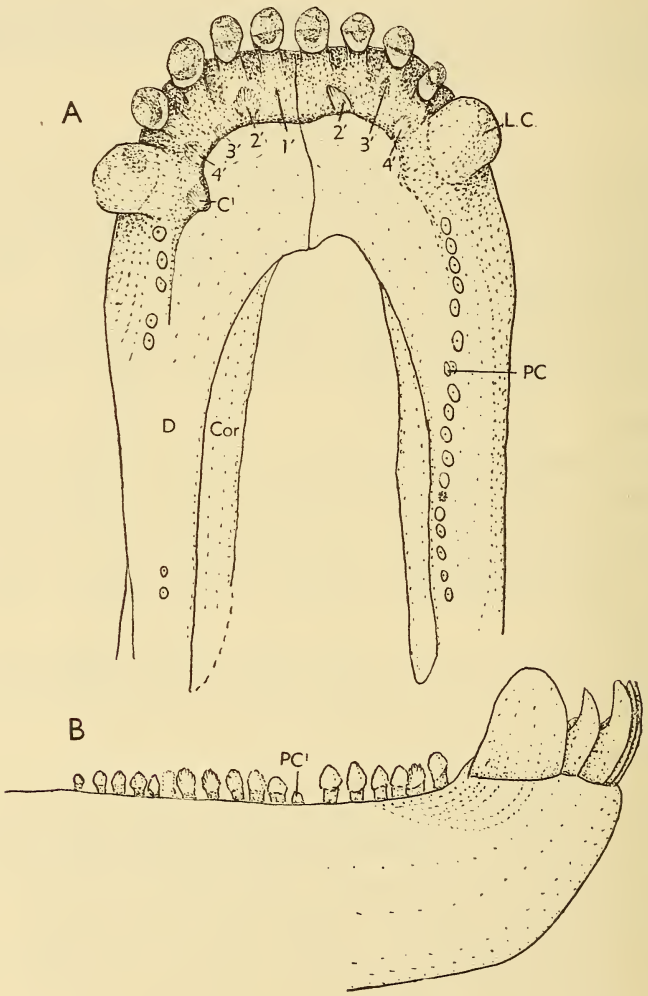


Fig. 12. *Parascapanodon* sp. S.A.M. 12213 B. ×¼.
A = dorsal view of mandibles.
B = lateral view of right mandible.

Incisors

The talons of the incisors are all lost except in No. 4 right. All the heels are very well preserved. The heel of No. 2 left has been worn fairly flat, whereas in all the others the lingual edge of the heel is still sharp; between this sharp ridge and the posterior face of the talon the face of the heel is hollowed out. In all, the inner corner of the heel is higher than the outer corner—the attritional face thus lies obliquely to the frontal plane.

On the left side replacing crowns lie in pockets of the alveolar wall of Nos. 2, 3, 4, and there is an empty pocket behind No. 1.

On the right side a strong replacing talon emerges obliquely from a pocket behind No. 2; the pocket behind No. 4 contains a tip, and empty pockets lie behind Nos. 1 and 3.

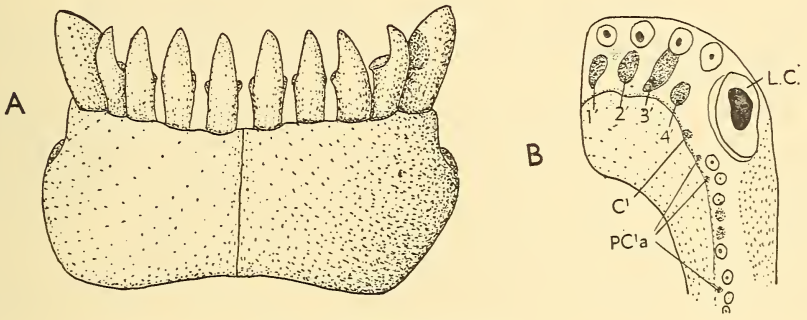


FIG. 13. *Parascapanodon* sp. ×¼.
A = S.A.M. 12213 B. Anterior view of the lower jaw.
B = S.A.M. 12213 C. Dorsal view of dentary.

Canines

All except the tips of both canines is preserved. The canines are large teeth, oval in cross-section. The diameters at the crown base are for the left 37 × 28 mm. and for the right 43 × 28 mm. Both canines are directed outwards. On the antero-internal face of the left canine there is a hollowed-out attritional face against which the upper 5th incisor worked.

The Postcanines

The spatulate crowns stand obliquely to the long axis of the skull; they are triangular in outline with sharp edges and are coarsely serrate. The outer face is convex and the inner fairly flat. The last five are appreciably smaller than their predecessors in the series. The postcanines are implanted on the inner upper edge of the dentary with a shallow groove externally for the reception of the upper postcanines.

C (fig. 13B). A weathered anterior part of the dentary shows the roots of all four functional incisors, but all four have reached the age at which they are to be shed. Lingually of each is a large empty alveolus from which the replacing

tooth has been lost. In No. 3 the alveolus, which housed the replacing tooth, has labially become confluent with the older alveolus housing the functional older tooth of the family. In the other three the alveoli of the replacing teeth are still separate from the older alveoli of the still functioning teeth.

The canine crown is broken off at its base where the diameters are 44×27 mm. The pulp cavity is large. The inner alveolar wall has a pocket for the replacing canine.

Evidence of nine postcanines is preserved; Nos. 4 and 5 are represented by empty alveoli and pockets for replacing teeth lie lingually of Nos. 1, 2 and 8.

Parascapanodon sp.

(Fig. 14)

S.A.M. 12219. Bosluiskraal, Laingsburg. Collected Boonstra 1959.

This specimen consists of a good left half of a snout and much of the postcranial skeleton.

The snout has its left half preserved in natural occlusion, but upper incisors Nos. 4 and 5 and the upper canine have fallen out of their respective sockets. The intermeshing of the incisors and canines is very clearly shown in this specimen. The first upper incisor is a very slender tooth. The lower canine is directed much outwards to pass outside of the maxillary edge.

A well-developed striate replacing crown lies in a pocket lingual of the right upper No. 1 incisor and a less developed one behind the left No. 1 incisor.

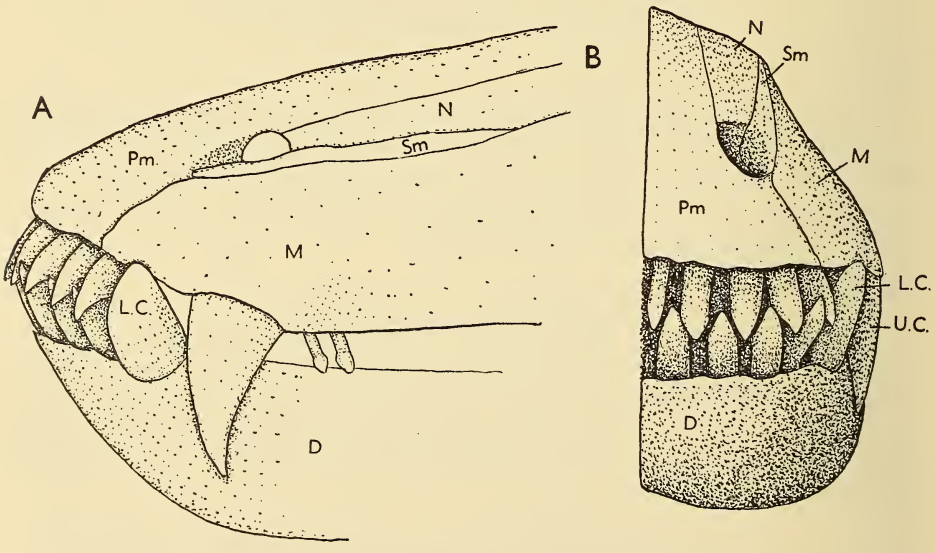


Fig. 14. *Parascapanodon* sp. S.A.M. 12219. ×½.
A = lateral view of snout. B = anterior view of the left half of snout as partly restored.

Parascapanodon sp.

S.A.M. 1204. Letjiesbos, B.W. Collected Whaits 1908.

This specimen (fig. 15) consists of the mentum of the lower jaw in which the incisors are fairly well preserved together with part of a canine crown and three postcanine crowns.

Incisors

Most of the crowns of the eight incisors are present; the heel is imperfect in one but present in the other seven where only the talons are partly lost, but these can be restored with confidence as is shown in the figures.

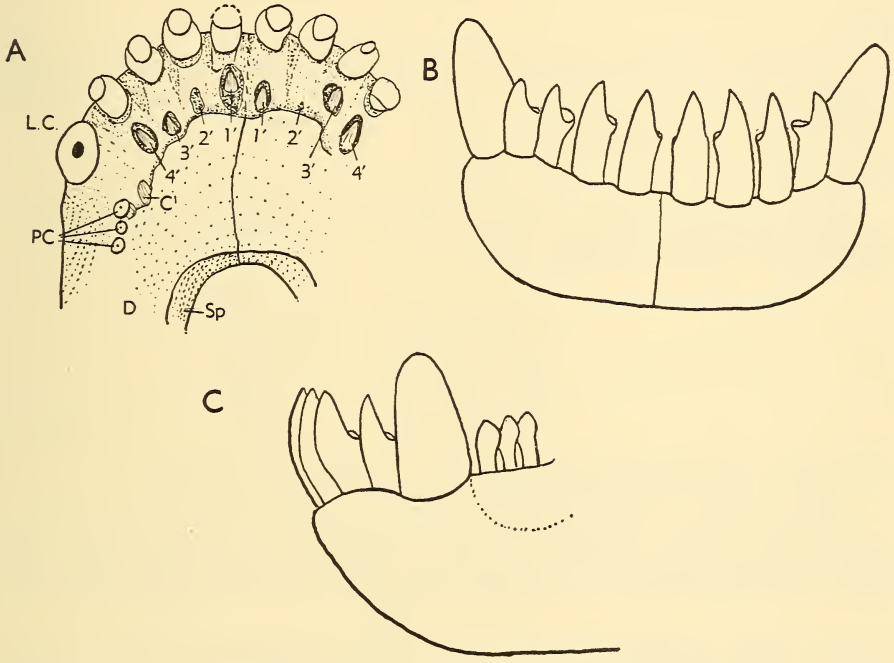


Fig. 15. *Parascapanodon* sp. S.A.M. 1204. ×¼.
A = dorsal view of lower jaws. B = anterior view of lower jaws. C = lateral view of the left mandible. Partly restored.

On the left side the four heels are excellently preserved in different stages of wear. No. 1 is worn smooth and nearly flat, in No. 4 there is still an indication of a lingual ridge, whereas in No. 3 and particularly in No. 2 the lingual ridge is still sharp and the face of the heel somewhat hollowed out. If the degree of wear is a criterion of age the order from oldest to youngest would be 1, 4, 3 and 2.

In the lingual wall of the alveolus of each functioning incisor there is a pocket. In pockets Nos. 1, 3 and 4, talons of the replacing incisors are present,

whereas that of No. 2 is empty. The replacing talons are in outline isosceles triangles, with longitudinally striate faces. According to the degree of development the order of eruption would be 1, 4, 3 and 2 agreeing with the degree of wear of the functional incisors.

On the right side the heel of No. 4 is damaged, that of No. 3 is worn flat, that of No. 1 fairly flat, and in No. 2 there is still a sharp lingual edge. The order of wear is thus 3, 4, 1, 2.

Lingually there are again four pockets in the alveolar wall. No. 2 is empty, whereas the others house replacing talons. The replacing order is 3, 4, 1 and 2.

Lingual of the replacing teeth the free upper edge of the flange of the dentary forms a high sharp edge.

Canines

The base of the left canine is preserved, with basal diameters of 33 and 25 mm. Lingual of the canine, at the edge of the dentary flange, a pocket contains the replacing canine tip.

Postcanines

Only three spatulate postcanines have their crowns preserved, with a replacing crown lying lingually of No. 1.

Jonkeriidae

Genus Jonkeria

Jonkeria cloetei

S.A.M. 731. Type Gamka River. Presented by Mr. Justice Cloete.

This type (fig. 16) consists of the anterior part of a left dentary, showing in section the roots of 4 incisors, 1 canine and the first four postcanines. The incisors were apparently fairly lightly built teeth. Lingually of each incisor the

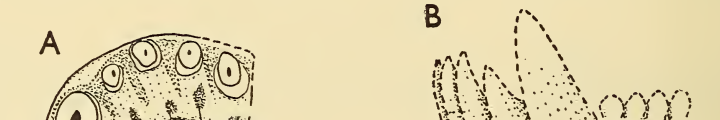


Fig. 16. *Jonkeria cloetei*. Type S.A.M. 731. ×¼.
A = dorsal view of left dentary.
B = lateral view of left dentary.

inner alveolar wall of the functioning incisors has been resorbed to form pockets through which the replacing incisors would in time have appeared. According to the development of these pockets the replacing order would have been 2, 4, 1, 3.

The base of the canine is only slightly oval in outline with diameters of 31 and 25 mm.

Lingually the alveolar wall of the functioning canine also shows a pocket and notch for the emergence of the replacing canine.

The roots of the four postcanines are large, with the first—with diameters of 7 and 10 mm.—smaller than those lying posteriorly.

The flange of the dentary with its free upper edge is well shown.

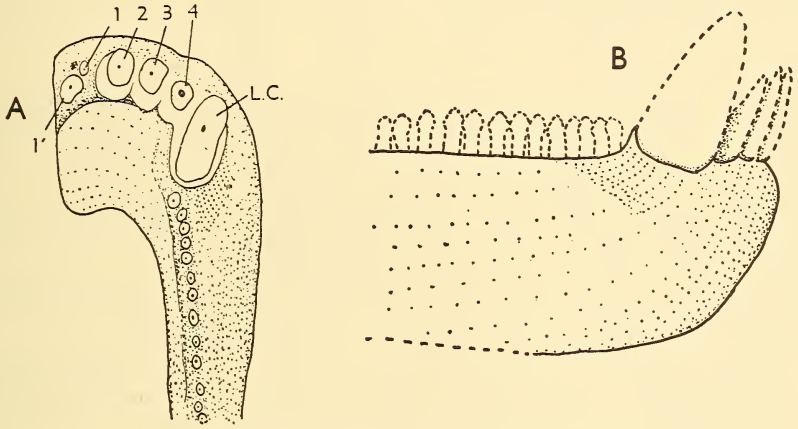


FIG. 17. *Jonkeria dubius*. Type S.A.M. 2759. ×¼.
A = dorsal view of right dentary.
B = lateral view of right dentary.

Jonkeria dubius

S.A.M. 2759. Type Platfontein of Abrahamskraal, P.A. Collected by Haughton 1913.

This type specimen (fig. 17) consists of the anterior part of a right dentary in which only the roots of the teeth are shown in section. There are four roots of functional incisors, No. 1 shows only the tip of a root lying in an alveolus from which it is just about shed, and intero-lingually lies a well-developed replacing incisor already occupying the functional alveolus. The other three incisors, as well as the canine, have the inner alveolar walls strongly developed as encasing sheaths. The flange of the dentary extends high up to almost meet the inner face of the alveolar walls at a high level.

The canine has a large root, which in outline is a long pinched-in oval with diameters 47 and 27 mm.

Of the postcanines the first 13 have their roots preserved. The first is the largest (diameter 9×8 mm. whereas the others have on the average diameters of 7×7 mm.).

The depression for the reception of the upper canine immediately behind the lower canine forms a deep anteriorly directed groove.

On the inner face of the dentary, where the splenial has fallen away, there are embedded an incisor and two postcanine crowns, possibly from the upper jaw.

Jonkeria haughtoni

S.A.M. 4343. Type Welgemoed, P.A. Collected Haughton 1916.

This type (fig. 18) consists of a fair skull without mandible, but with much of the postcranial skeleton.

Incisors

On the left the tip of the premaxilla has been lost and only sections of the roots of the five incisors can be seen at depth. On the inner alveolar face there are pockets for the replacements of Nos. 2 to 5 with crown tips of Nos. 3 and 4 lying in their pockets. The replacing order appears to be 3, 4, 5, 2, 1.

In the right premaxilla the crowns of Nos. 4 and 5 are very well preserved, whereas the other three are broken off at the alveolar border.

As preserved the incisors are directed very much anteriorly, but most of this is due to the dorso-ventral crushing of the skull after death.

The two preserved crowns differ from those known in other forms. In No. 4 the inner face of the talon runs obliquely from the heel to the tip without the usual distinctive face on the heel itself, which in other forms is either flat or hollowed out. In No. 5 this sloping inner face is also evident, but in this tooth it is bipartite—the outer and greater part is for the reception of the lower canine.

Lingually of the right incisors there are four pockets in the alveolar wall for the replacements 2–5; in Nos. 2 and 4 there lie the striate tips of the talons of the replacing teeth. The replacing order appears to be 4, 2, 5, 3, 1.

Canines

In the left maxilla there is an irregular empty alveolus from which the canine has dropped out and lingually of this there is a shallow pocket for its replacement. As this pocket contains no replacing crown it is reasonable to assume that the functional canine has not been naturally shed but lost *post mortem*, otherwise the animal would have been without a functioning canine for an inconveniently long time.

The right canine has its crown very well preserved. As preserved, it is rather short and greatly recurved and directed much outwards—this may be unnatural and really due to the aforementioned dorso-ventral crushing the skull has undergone. At its base the crown has diameters of 42 and 24 mm. and a crown length of at least 60 mm.

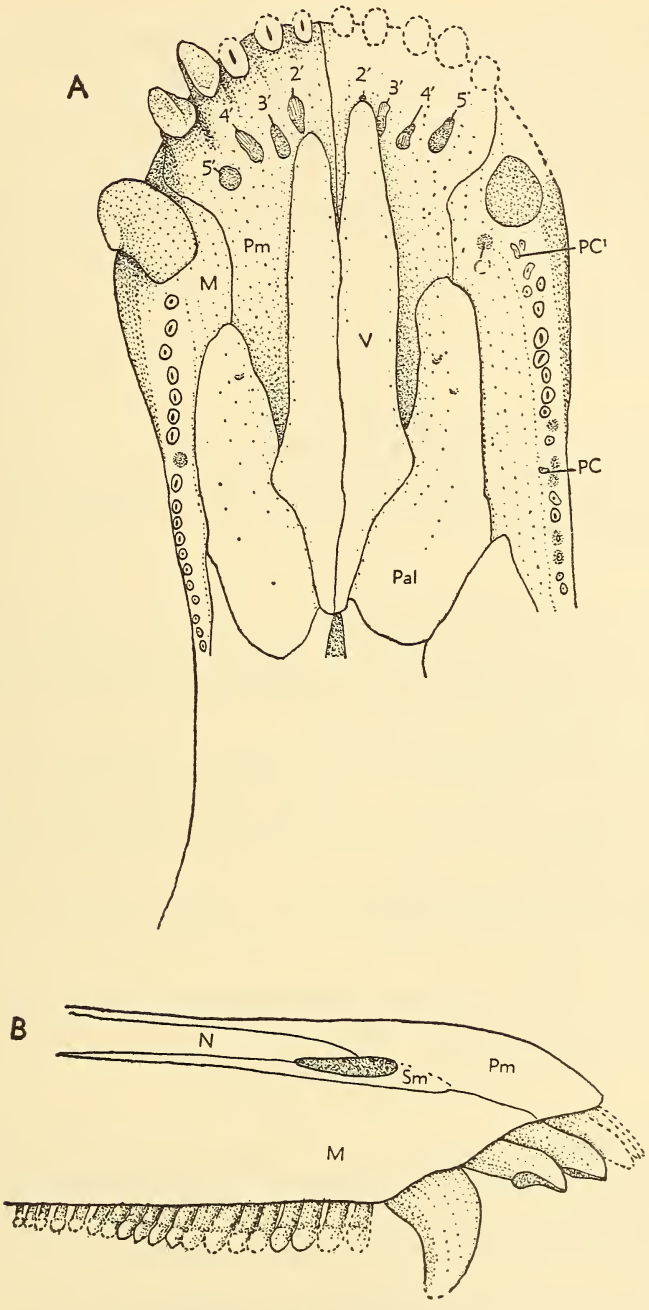


FIG. 18. *Jonkeria haughtoni*. Type S.A.M. 4343. ×½.
A = ventral view of the anterior half of the palate.
B = lateral view of the right side of the snout.

Postcanines

On the right side some of the crowns are preserved, whereas on the left only the roots are to be seen in section. The backward slant of the preserved crowns is again due to the crushing the skull has undergone.

On both maxillae there is evidence of 19 postcanines, occupying on the right 187 mm. and on the left 188 mm.

On the right side no replacing teeth can be determined and No. 8 is represented by an empty alveolus. On the left there are replacing teeth lingual of Nos. 1 and 3 and lingual to the empty alveoli of Nos. 12 and 13 is another replacement. Alveoli Nos. 16 and 17 contain two small tips and alveoli 10, 12 and 13 are empty.

Jonkeria boonstrai

S.A.M. 9079. Rietkuil, B.W. Collected Boonstra 1929.

This specimen (figs. 7 and 8), which has been referred to Janensch's type, consists of a weathered disarticulated skull, with good upper jaws and part of the mandibular ramus.

Incisors

In the right premaxilla the roots of five incisors are present, with pockets in the inner alveolar walls of Nos. 1, 3 and 5, in which lie the crown tips of replacements 1 and 3, whereas no crown tip has as yet been formed for No. 5. The replacement order is 1, 3, 5, ?, ?.

On the left side the roots of Nos. 1, 4 and 5 are definitely present, whereas those of 2 and 3 are indefinite. Four pockets in the inner alveolar wall can be seen, each housing a tip of the replacing tooth. The replacement order is 5, 2, 4, 1, 3. The lingual face of replacing No. 5, which is well developed, shows coarse striae, and the edge, which in outline is elongated triangular, is coarsely serrate with blunt rounded serrations.

Canines

The canine roots have the following diameters: left 40 × 39 mm., right 40 × 30 mm. Lingually of each canine there is a pocket in the alveolar wall indicating where the replacing canines are to appear.

Postcanines

Both maxillae show a good series of roots of functional postcanines and crowns of the replacing set. On both sides the complete set consisted of 18 teeth, with the first larger than the rest, which gradually decrease in size posteriorly. On the right side the series measures 169 mm. and on the left 170 mm. in length.

On the right side Nos. 9, 10 and 13 are represented by empty alveoli and lingual to Nos. 1, 2, 5, 8 and 11 are pockets for replacements and lingual to 6, 9, 10, 13 and 15 there are tips of the replacing teeth showing.

On the left side No. 6 has an empty alveolus, linguo-anteriorly of No. 1 there is a fairly large pocket for a replacing tooth, and lingually of Nos. 1, 2, 3, 5, 6, 10 and 11 there are replacing crowns. The large pocket may be for a tooth anterior to the one I am considering the first postcanine, which would then be the second.

The erupted crowns of the replacing postcanines are triangular to spatulate in outline with serrate edges composed of blunt rounded cusplets and the inner face is finely striate.

The Lower Jaw

Of the anterior part of the left dentary (fig. 8) I have cut three slabs in frontal section to show the roots of the teeth in use and the stages of development of the replacing tooth.

Section A shows the roots of the four functioning incisors, the canine and the first postcanine. Lingually there are cavities behind Nos. 2 and 4 which contain the beginnings of the cusps of the replacing incisors. Lingually of Nos. 1 and 3 there are empty cavities as yet not showing any dentine of replacing Nos. 1 and 3. Lingual of replacing No. 2 there is an empty cavity presumably for the successor to replacement No. 2.

Lingually of the canine root is a pocket which contains the tip of the crown of the replacing canine lying loosely in the pocket.

Section B still shows the functioning teeth roots; behind No. 2 a crescent of dentine in a large cavity is that of replacement No. 2; replacement No. 1 is represented by an empty cavity and lingual of replacement 2 the cavity for its replacement is also still empty. Two empty cavities situated far lingually may be for the second replacements of 3 and 4.

The replacing canine is here seen to occupy the antero-labial part of a cavity.

Section C. Besides the roots of the functioning teeth this section shows that labially of the root of the functioning No. 4 incisor there lies the still unresorbed root remnant of an older fourth incisor. The two empty cavities are presumably those of replacement No. 4 and the second replacement of No. 2.

Jonkeria vanderbyli

S.A.M. 11884. Skroefpaal, P.A. Collected by Boonstra and Rossouw in 1948.

This fairly well-preserved and complete skull, with the lower jaws preserved in natural occlusion, has been referred to Broom's type (figs. 19 and 20).

In separating the lower jaws from the upper, the crown of the right lower canine has broken off and lies in its occlusional position, viz. between the upper canine and the 5th upper incisor; similarly the crown of the upper right canine is broken off near its base and lies in its occlusional position, viz. labial to the first 4–5 lower postcanines.

Incisors

Both premaxillaries carry five functional incisors. The No. 1 pair are smaller teeth lying close together. On the left side the inner alveolar wall is fenestrated behind Nos. 1, 3, 4 and 5, and in each pocket lies the crown of a replacement tooth, triangular in outline and with its inner face striate. The replacement order is 5, 1, 3, 4, 2.

In the dentaries four incisors are preserved on the left side and three on the right side—No. 1 being lost. No replacements have been exposed.

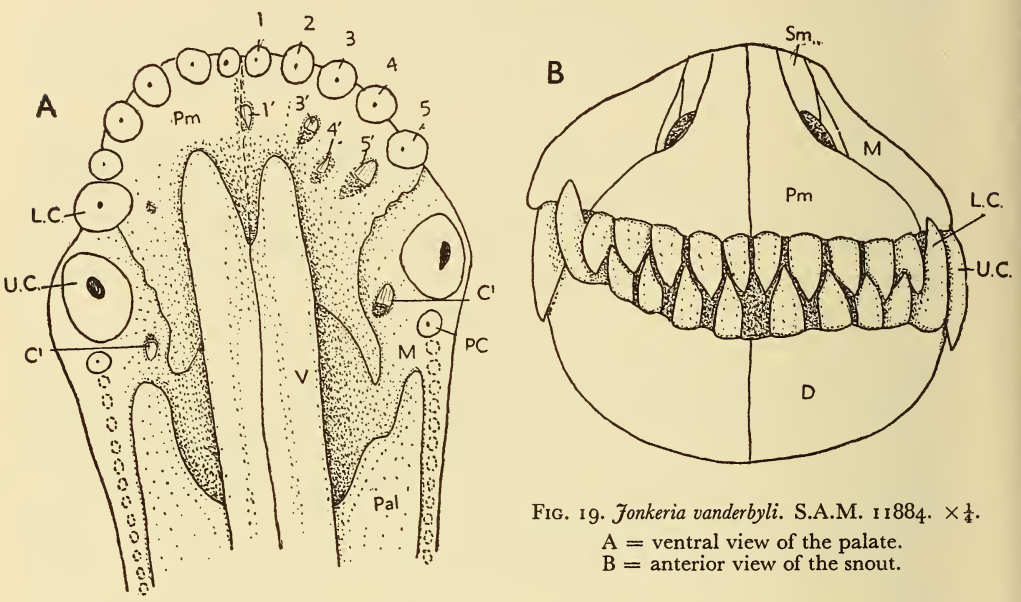


FIG. 19. *Jonkeria vanderbyli*. S.A.M. 11884. ×¼.
A = ventral view of the palate.
B = anterior view of the snout.

This specimen again very clearly shows the intermeshing of the upper and lower incisors. The pair of slender upper Nos. 1 having their talons passing in between the lower Nos. 1, with the outer halves of their heels meeting the inner halves of the heels of the lower incisors; upper No. 2 passes between lower Nos. 1 and 2, and No. 3 between 2 and 3; No. 4 between 3 and 4, and No. 5 between lower 4 and lower canine.

Canines

The upper canines are large, pointed and curve backwards. The length of the crown is at least 90 mm. and the basal diameters are right 49×36 mm. and left 45×34 mm.

In the pockets lingual of each canine lies the tip of the replacing canine.

The lower canines are smaller than the upper and are directed forwards and outwards. The basal diameters are right 29×27 mm. and left 27×27mm., and the lengths 50 mm. and 45 mm.

The lower canines intermesh between the upper fifth incisor and the upper canine.

Postcanines

The upper postcanines are very poorly preserved—in fact, most have fallen out after death and their alveoli are difficult to determine. It is clear, however, that on both sides the first postcanine is much larger than those further back.

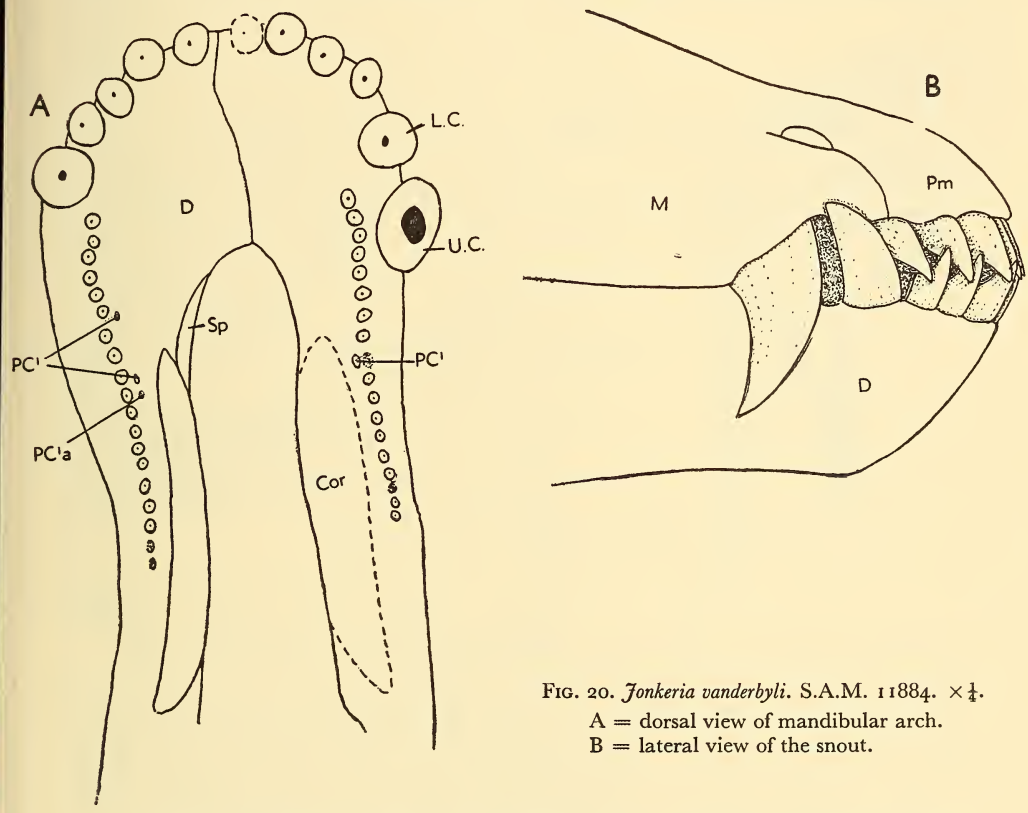


FIG. 20. *Jonkeria vanderbyli*. S.A.M. 11884. ×¼.
A = dorsal view of mandibular arch.
B = lateral view of the snout.

In the dentaries the postcanines are fairly well preserved. On the right side 18 teeth occupy 180 mm.—Nos. 9 and 16 are represented by empty alveoli and lingual of alveolus No. 9 lies a replacing crown. In the left dentary 19 teeth occupy 180 mm. Nos. 18 and 19 are represented by empty alveoli. Lingual to Nos. 6 and 9 lie replacing crowns and lingual to No. 10 is an empty alveolus.

Jonkeria truculenta

S.A.M. 12030. Bosluiskraal, Laingsburg. Collected Boonstra 1956.

This specimen (figs. 5, 21, 22, 23, 24, 40 and 41) consists of a fairly good though somewhat distorted skull, which I am referring to van Hoepen's species.

In both upper and lower jaws of the left side the dentition is particularly well preserved and on the right side sectioning shows complementary features. On the left side the dental formula is: i $\frac{5}{4}$, c $\frac{1}{1}$, pc $\frac{18}{18}$.

Incisors

In the left premaxilla (fig. 21) the root only of No. 1 is preserved, whereas the other four incisors have most of the crowns present. The heels of Nos. 3 and 4 are worn flat, whereas in No. 2 the heel has a fairly sharp ridge, bounding a hollow lying between it and the talon, and in No. 5 the inner face of the talon is bipartite with the outer part, which receives the lower canine, the greater.

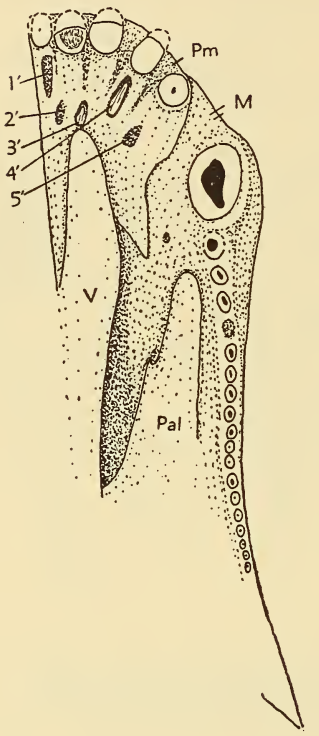


FIG. 21. *Jonkeria truculenta*. S.A.M. 12030. ×$\frac{1}{4}$. Ventral view of left half of snout.

Lingual of each incisor there is a pocket in the inner alveolar wall of the functioning incisors of which Nos. 3 and 4 house replacing tips and the others as yet empty. The replacing order is 1, 4, 3, 5, 2.

In the right premaxilla I have cut two frontal sections (fig. 24B):

1. shows the roots of five incisors with No. 1 a slender tooth. Five lingual pockets are present, of which Nos. 2, 3 and 4 contain the talons of the replacing incisors and the other two are empty.
2. again has the roots of the five functional incisors; cavities 2 and 3 contain replacement teeth and Nos. 1 and 4 are empty.

The replacing order is 2, 4, 3, 1 and 5.

In the left dentary (fig. 23) four incisors are preserved; No. 4 has lost its crown; No. 3 is well worn so that the occlusial surface of the heel is smoothly flat and the talon so worn on its lingual face that all that remains of the talon is a weak cone; No. 2 is much less worn and has a fairly strong talon; No. 1 just shows the tip of a talon which appears to be piercing a plug of cancellous bone filling the alveolus.

Three frontal sections of the right dentary (fig. 24A) show:

1. Just below the alveolar level four incisor roots; lingually of Nos. 2 and 4 there are pockets in whose anterior part lie sections across the talons of the replacing teeth; lingually of No. 3 is an empty pocket. The flange of the dentary lying lingually of these pockets is seen as a loose strip of bone.

2. Lying 9 mm. deeper this section shows replacement No. 2 lying in its pocket, a cavity housed the replacement of No. 3 and cavity No. 4 is empty.

   Lingually of the functional canine root lies a pocket housing the replacing canine.

3. Here an empty cavity for replacement of No. 1 is seen and a replacement of the third postcanine.

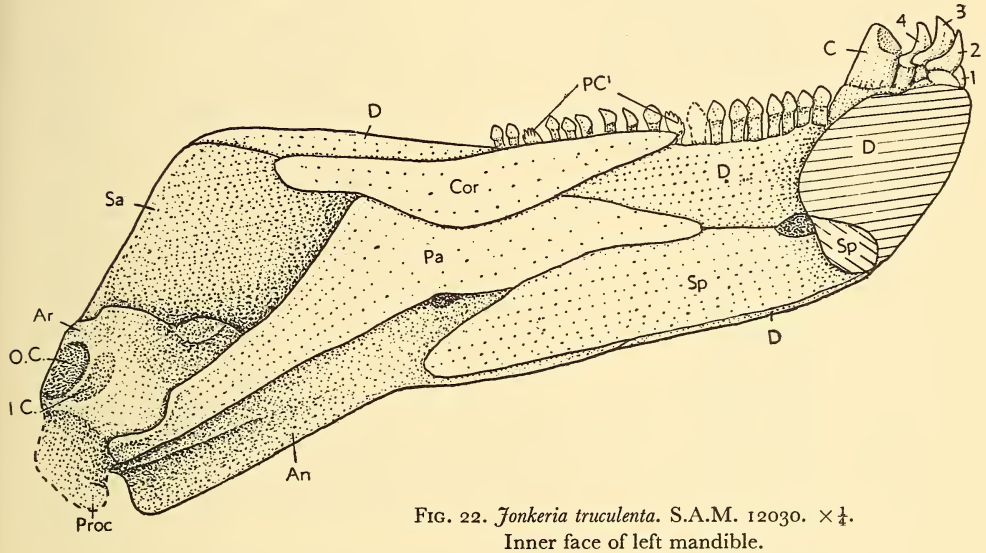


FIG. 22. *Jonkeria truculenta*. S.A.M. 12030. ×¼.
Inner face of left mandible.

Canines

The left upper canine is beautifully preserved. The crown length is 90 mm. and at its base its diameters are 42 and 29 mm. It is thus a long, moderately strong tooth and has only a moderate posterior curvature; its posterior face is rounded with no indication of a cutting edge. The right upper canine has diameters of 50 and 24 mm. A small pocket for the left replacing canine lies linguo-posteriorly of the functional canine.

The left lower canine is fairly well preserved; its length is 41 mm. and its basal diameters are 24 and 31 mm. It is thus quite a moderately sized tooth. It is directed both forwards and outwards. Just behind its tip there is an oval hole which is a result of resorption of the dentine. Its antero-dorsal face is excavated to form a heel bearing some similarity to that typical of the incisors. The fifth upper incisor fits with the postero-external part of its heel into this heel of the lower canine. The mode of intermeshing is thus as is typical of the incisors. Lingually of the canine base there is the usual notch in the flange of the dentary for the replacing canine.

In the right dentary, sectioning shows a canine root with diameters 30×20 mm. and a pocket containing the tip of the replacing canine.

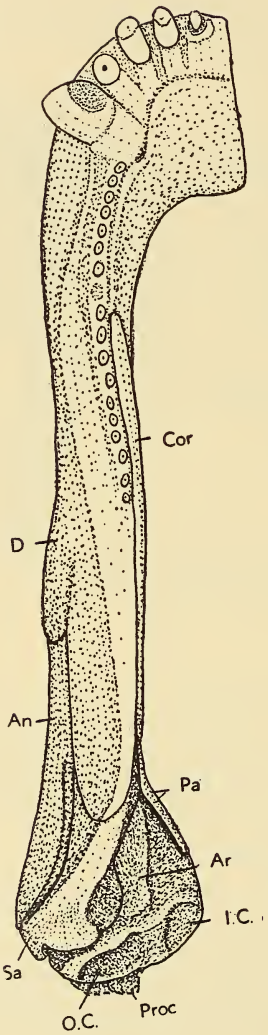


FIG. 23. *Jonkeria truculenta.*
S.A.M. 12030. ×¼.
Dorsal view of left mandible.

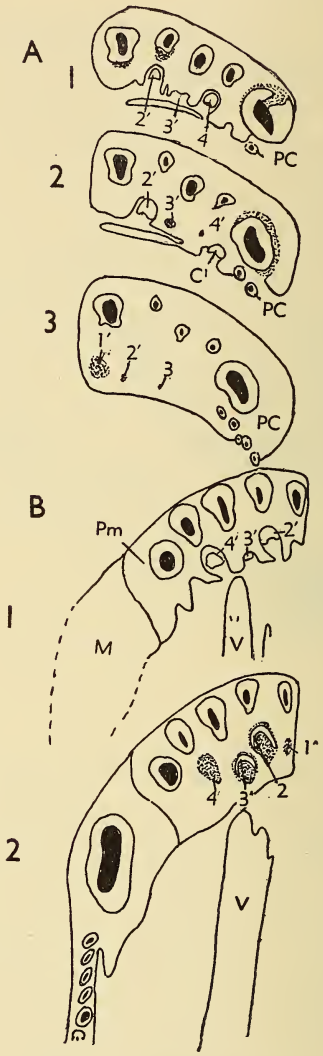


FIG. 24. *Jonkeria truculenta.*
S.A.M. 12030. ×¼.
A = Three consecutive frontal sections through the right dentary.
B = Two frontal sections through the right upper jaw.

Postcanines

In the left upper jaw (fig. 21) a well-preserved series of postcanines follows immediately on the canine without any diastema. The length of the series is 179 mm. and there were 18 teeth. No. 1 is much larger (diameters 13×11 mm.) than its immediate successors (diameters 10×8 mm.) and then the teeth gradually decrease in size posteriorly (the last 5×4 mm.). No. 4 is represented by an empty alveolus and No. 11 by the crown of a replacing tooth.

The bulbously spatulate crown is very well shown in a number of teeth. The crowns lie obliquely to the long axis, with the posterior edge directed outwards and the anterior edge inwards. The posterior edge is sharp and is separated from the main bulbously swollen part of the crown by a shallow longitudinal groove. The inner face of the crown is flattened.

In the left dentary (figs. 22, 23) a good set of crowns has been exposed from the lingual side. The series of 18 teeth occupy a length of 179 mm. No. 8 is represented by an empty alveolus. No. 9 is represented by a nearly fully erupted crown of a replacing tooth and so is No. 16. The functional lower postcanines show on their lingual faces a moderately developed heel forming a cingulum at the junction of crown and root; above this the inner face of the crown is concave with longitudinal striae.

In the unworn replacing teeth those striae are more definite and extend to the edges of the crown, which thus become serrate with rounded cusplets.

The first 4–5 lower postcanines lie lingually of the upper canine in occlusion and the rest lingually of the upper postcanines with no indication of any intermeshing.

As the upper and lower series of postcanines occupy the same length of jaw, follow immediately on their respective canines, and the lower canine lies in front of the upper canine, it follows that the posterior upper postcanines (four of them) have no lower antagonists. The first upper postcanine lies labially of the 6th lower postcanine to constitute its antagonist.

Jonkeria ingens

S.A.M. 11573. Klein-Koedoeskop, B.W. Collected Boonstra 1940.
S.A.M. 11574. Klein-Koedoeskop, B.W. Collected Boonstra 1940.
S.A.M. 11575. Klein-Koedoeskop, B.W. Collected Boonstra 1940.

Twenty years ago I excavated three quite good skulls lying together in a thin sandstone layer. In all three, few of the crowns of the teeth are preserved. Of 11573 (fig. 25) I have cut a frontal section across the premaxillaries and the other two have been serially cross-sectioned for the study of the internal structure which is being published shortly. What has been seen of the teeth confirms what has been described in the foregoing pages for other *Jonkeria* species, with little of taxonomic importance.

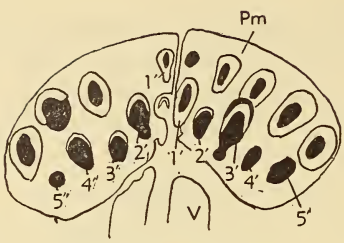


Fig. 25. *Jonkeria ingens*.
S.A.M. 11573. ×¼.
Frontal section through the premaxillaries to show the replacing incisors.

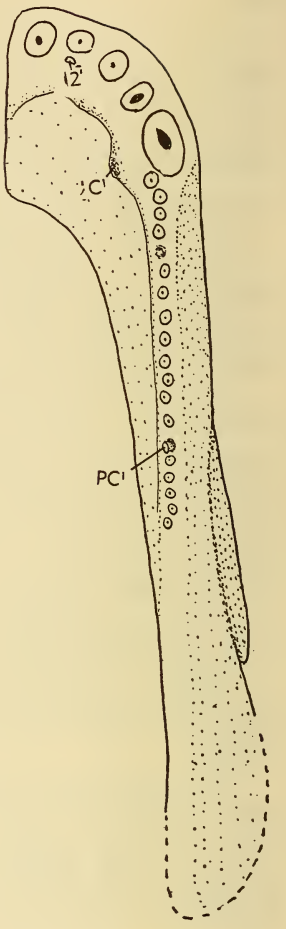


Fig. 26. *Jonkeria ingens*.
S.A.M. 12248. ×¼.
Dorsal view of right dentary.

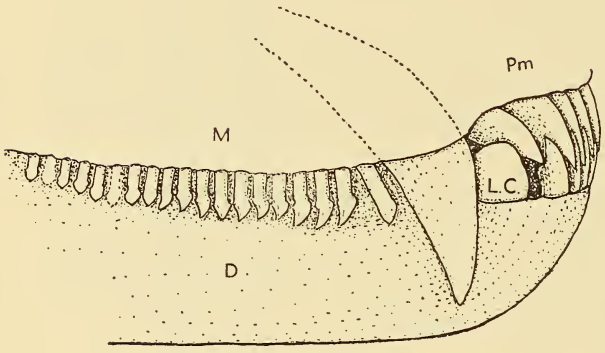


Fig. 27. *Jonkeria* sp. S.A.M. 11486. ×¼.
Lateral view of the right side of the snout.

Upper Incisors

In the right premaxilla the roots of the functional Nos. 2, 3, 4 and 5 are present with No. 1 represented by an empty alveolus. Lingually of these lie a well-developed replacement No. 1 and 3, the former in a separate alveolus and the latter growing into the old alveolus; replacement No. 2 is just developed and for replacements of Nos. 4 and 5 there are empty alveoli.

In the left premaxilla there is no trace of the functional No. 2, and No. 4 is being resorbed, Nos. 3 and 5 have well developed roots and so has the slender No. 1. Replacement No. 1 is seen in its pocket and Nos. 2, 3, 4 in separate cavities, and for No. 5 there is an empty alveolus.

S.A.M. 12248. Skoppelmaaikraal, Laingsburg. Collected Boonstra 1959.

This specimen (fig. 26) consists of the weathered disarticulated bones of both jaws, of which the right dentary is almost complete and shows cross-sections of the roots of the whole set of teeth.

Incisors

There are four functioning incisors and lingual to No. 2 there is an erupting talon of a replacing tooth lying in a separate alveolus.

Canines

At its base the canine has the diameters 37 × 26 mm. and, lingual to it, above the flange of the dentary, lies the pocket for its replacement.

Postcanines

There were 19 postcanines occupying 189 mm. of the jaw. The first postcanine lies immediately behind the canine. No. 5 is represented by an empty alveolus and lingual to the empty alveolus of No. 14 lies its replacing crown.

Jonkeria sp.

S.A.M. 11486. Mynhardtskraal, B.W. Collected Boonstra 1940.

This specimen (fig. 27) consists of a fair snout of which the left half has been serially cross-sectioned and the right half prepared externally to show the dentition.

Incisors

The crowns of the five right incisors are preserved in a fair state. The postero-lateral face of No. 5 receives the antero-internal attritional face of the lower canine, which clearly intermeshes between it and the upper canine.

In the right dentary the first three incisors are functional, whereas No. 4 has fallen out, but has a well-developed replacement crown occupying the lingual part of the alveolus. The tip of No. 2 replacement is also well erupted and pockets for Nos. 1 and 3 are present. The replacement order is 4, 2, 3 and 1.

Canines

The upper canine is a large conical tooth only slightly recurved. The crown is 82 mm. in length and the basal diameters 50 × 22 mm. The root is very large with a roomy pulp cavity, its length is at least 100 mm.

The lower canine is short (crown length 32 mm.) and weak with basal diameters 26 × 21 mm. It is directed outwards to lie between the upper canine and the upper fifth incisor against which it bears.

Postcanines

The upper postcanines follow on the canine without diastema. There is evidence of 19 teeth occupying 183 mm. This specimen clearly shows that the

first postcanine differs from the rest; it is directed parallel to the direction of the canine and it appears to be more pointed than spatulate. Its antero-posterior diameter is 14 mm. as against 11 mm. in the second postcanine and 7 mm. in the last postcanine. Nos. 14 and 18 are represented by empty alveoli with presumably replacements lying lingually.

In the dentary there are also 19 postcanines occupying a distance of 176 mm. The postcanines have their crowns situated obliquely to the sagittal plane.

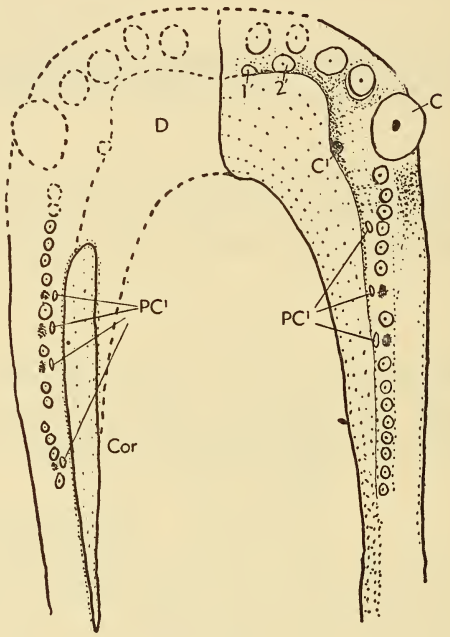


Fig. 28. *Jonkeria* sp. S.A.M. 5017. ×¼.
Dorsal view of mandibular arch.

This specimen again clearly shows that, since the postcanines follow immediately behind both upper and lower canines and the lower canine passes anterior to the upper one, the lower series cannot extend so far posteriorly as the upper series even if they were of the same length. In fact the lower series is 7 mm. shorter and ends 50 mm. anterior to the level of the last upper postcanine. The last 6 upper postcanines thus have no antagonists and the first 4–5 lower postcanines have the upper canine as antagonist.

Jonkeria sp.

S.A.M. 5017. Abrahamskraal, P.A. Collected Haughton 1917.

This specimen (fig. 28) consists of a poorly preserved skull lacking upper jaws and two imperfect mandibular rami.

Incisors

On the right dentary there are roots of the four incisors and lingually of Nos. 1 and 2 replacing talons are developed. The flange of the dentary extends high up behind the replacing teeth as in *Jonkeria dubius*.

Canines

The base of the canine crown is seen in section and the diameters are 35 × 28 mm. Lingually there is a pocket in the alveolar wall and a notch in the flange of the dentary for the emergence of the replacing canine.

Postcanines

On the right side there is evidence of a series of 17 postcanines occupying 173 mm. Nos. 7 and 9 are represented by empty alveoli lingual to which are the crowns of their replacements. A further replacing crown lies lingual of No. 4.

On the left side the dentary is incomplete anteriorly to the 3rd postcanine. Posteriorly there is evidence of 16 postcanines occupying 140 mm. Nos. 7, 9, 11 and 17 are represented by empty alveoli lingual to which lie erupting crowns of their replacements.

Jonkeria sp.

S.A.M. 9161. Wakkerstroom of Wolwefontein, P.A. Collected Boonstra 1929.

The specimen (fig. 9) consists of parts of a broken-up skull, including pieces of the upper jaw and much of the mandibular arch.

Incisors

In the right dentary four functional incisors are present, but both Nos. 1 and 3 are on the point of being shed with their respective replacements already well developed. This is particularly so in No. 1, where a lucky fracture shows the mode of replacement very well (fig. 9B). The root of functional No. 1 is nearly resorbed and in its alveolus lingually to the remains of the root lies the already well-developed replacement. The pulp cavity of functional No. 1 is closed, whereas that of its replacement is large and widely open. The talon of the replacing tooth is well shown as well as the hollowed face of the heel with its rounded lingual ridge. Lingual to the heel the inner alveolar wall is seen in section and is thus a fairly thin sheet of bone; lingual to this there is a deep groove and still further lingually the flange of the dentary with its free upper edge is seen in section.

In the left dentary No. 1 incisor is represented by an empty alveolus in whose lingual part there lies the talon of the replacing tooth.

Canines

On the left a section across the base of the canine crown is seen, which is much laterally compressed with diameters 29 and 19 mm.; on the right there is a broken crown directed much outwards with basal diameters 32 × 24 mm.

Postcanines

On the right a series of 16 postcanines occupying 154 mm. is preserved. No. 1 is much larger (diameters 11 × 8 mm.) than its successors in the series. Nos. 4, 11 and 13 are represented by erupting alveoli with replacing crowns lingual to Nos. 4 and 13. No. 12 is the remains of the root of a functional tooth with an erupting alveolus lingual to it.

Jonkeria sp.

S.A.M. 9162. Wakkerstroom of Wolwefontein, P.A. Collected Boonstra 1929.

This specimen (figs. 4 and 29) consists of the anterior half of a skull in which the bones of the jaws have become partially disarticulated and shifted from their natural position. The figures given here are reconstructions.

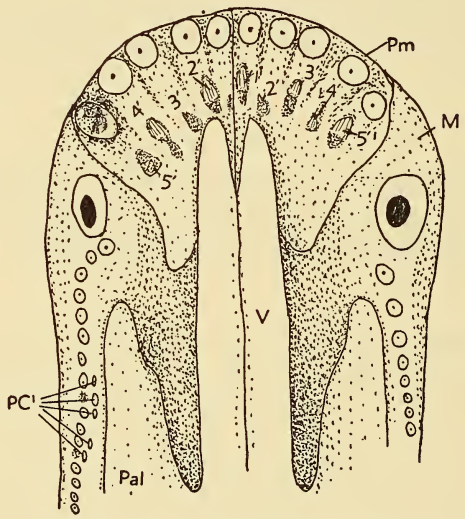


Fig. 29. *Jonkeria* sp. S.A.M. 9162. × ¼.
Ventral view of the anterior part of the palate.

Incisors

In both premaxillaries the crowns of the incisors are considerably damaged; there are five pairs with the first pair slender and situated close together. This specimen shows the intermeshing of the upper incisors with the lower, as already described, very well.

On both sides the five pockets for the replacing incisors have been exposed.

In the right premaxilla the replacing crowns of Nos. 2 and 4 are visible in their pockets and they show the elongate inner face of the talons with the edges coarsely serrate. The replacing order is 2, 4, 5, 3, 1.

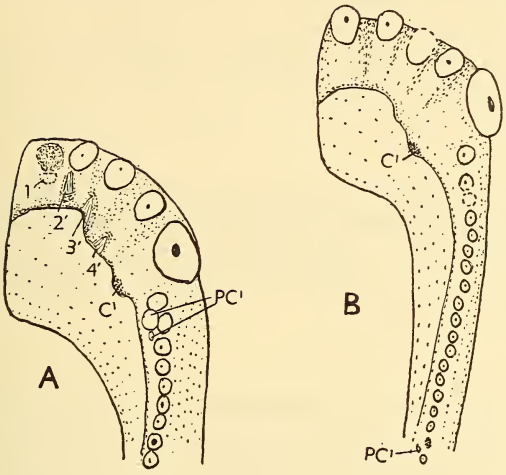


FIG. 30. *Jonkeria* sp. $\times\frac{1}{4}$.
A = S.A.M. 11980. Dorsal view of right dentary.
B = S.A.M. 12021. Dorsal view of right dentary.

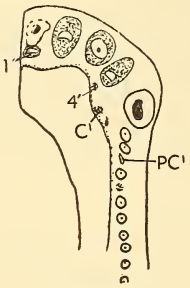


FIG. 32.
Jonkeria sp. Juv.
S.A.M. 12151. $\times\frac{1}{4}$.
Dorsal view of right dentary.

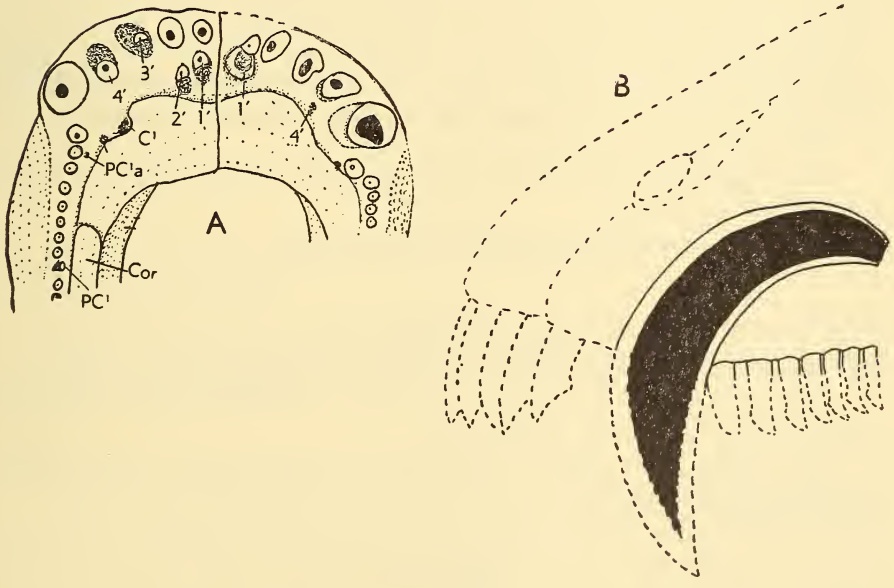


FIG. 31. *Jonkeria* sp. S.A.M. 12024. $\times\frac{1}{4}$.
A = dorsal view of the anterior end of the mandibular arch.
B = a fracture through the maxilla gives a longitudinal section through the left canine.

In the left premaxilla the replacing crowns are visible in pockets Nos. 1, 3, 4 and 5, and the replacing order is 5, 1, 3, 4 and 2.

On the right side the incisors in the dentary are in the natural occlusional position with the upper incisors, and the intermeshing of the four lower with the five upper incisors is very definite.

Canines

The lower canine in occlusion lies in front of the upper canine passing outwards in between this and the upper fifth incisor. It is a moderately sized tooth with its greater basal diameter 29 mm. On the right side there is a large upper canine very little recurved; the length of the crown is at least 80 mm. with basal diameters of 43 and 28 mm.

Postcanines

The crowns of the postcanines are only preserved in some of the more anterior teeth. They have the usual swollen spatulate crowns lying obliquely to the long axis. On the right maxilla there is evidence of 17 teeth occupying 142 mm. Nos. 9 and 10 are represented by empty alveoli and lingual to Nos. 8, 9, 10, 12 and 13 replacing teeth are present.

Jonkeria sp.

S.A.M. 11980. Lammerkraal, P.A. Collected Haughton 1916.

This right dentary (fig. 30A) shows the incisor roots of Nos. 2, 3 and 4 and an empty alveolus for No. 1, lingual of which is a well-developed talon of the replacing tooth; pockets contain the replacements of Nos. 2, 3 and 4.

The canine at its base measures 34 × 26 mm.

Nine closely packed postcanine roots are preserved with replacements lying lingually of Nos. 1 and 2.

This may be a second specimen of *Jonkeria cloetei*.

Jonkeria sp.

S.A.M. 12021. Skoppelmaaikraal, Laingsburg. Collected Boonstra 1956.

This specimen (fig. 30B) consists of a left premaxilla and a right dentary in which the teeth are seen in cross-section.

Four functioning incisors, a canine and 19 postcanines are evident with a replacing 18th postcanine.

Jonkeria sp.

S.A.M. 12024. Skoppelmaaikraal, Laingsburg. Collected Boonstra 1956.

The specimen (fig. 31) consists of weathered broken pieces of both upper and lower jaws.

The interesting features shown are: in the left dentary incisors Nos. 1 and 2 are functional, with well-developed talons of their replacements lying lingually; in Nos. 3 and 4 well developed replacing talons are visible lying loosely in the alveoli. In the right dentary No. 1 alveolus is occupied by a very well-developed replacing tooth, which is just coming into use. The inner edge of the heel is unworn and is sharp with fine striae and the face of the heel is deeply hollowed out.

In a piece of the left maxilla fracturing has revealed the root of the canine in longitudinal section. The root is curved strongly posteriorly and has a roomy pulp cavity, which opens on to the inner maxillary face just behind the strong internal maxillary bulge.

Jonkeria sp.

S.A.M. 12151. Danskraal of Bloudraai, P.A. Collected Boonstra 1957.

This small dentary (fig. 32) is of interest in that it appears to be that of a young reptile.

The canine is small with basal crown diameters 29 and 22 mm.

Notwithstanding its assumed youth there is already an empty postcanine alveolus (No. 5), but No. 3 is a newly erupted crown.

No. 1 incisor has a pulp cavity widely open at its base, but lingually in the same alveolus there is already a replacing talon with an undeveloped root. One can thus with reason state that in youth the incisor replacement occurs rapidly and probably often. In alveoli Nos. 2 and 4 lie talons just appearing above the alveolar border, and in No. 3 there is a root lying loosely in the alveolus. Lingual to No. 4 there is already a pocket for the next tooth.

Jonkeria sp.

S.A.M. E. This specimen bears a field number E, but both the collector and the locality are unknown.

The specimen (figs. 2 and 3) consists of a left premaxilla and maxilla not in articulation with four incisors broken away from the premaxilla and one root still in the premaxilla.

Incisors

Of the incisors there is preserved: the root of No. 5; No. 4 has part of the root and crown preserved and this is in position in the piece of premaxilla, which also holds Nos. 3 and 2 in natural relation and the latter two consist of good crowns with only the tips missing; No. 1 consists of a detached crown.

All the incisors have the same general build although differing somewhat in size and proportions.

Measurements as reconstructed:

	1	*2*	*3*	*4*	*5*
Total height of crown and root	?	110	110	?	?
Height of crown	45	53	53	?	?
Maximum width of talon	14	15	18	?	?
Maximum width of heel	13	16	17	?	?
Ant.–post. length over heel	31	30	29	24	?
Height of talon	26	32	30	?	?

No. 1 is thus shorter and more slender than the others.

In the incisors the crown and root are roughly two curved cones of about equal size with their bases applied to each other, so that in side view they together have an outline resembling a sickle moon.

At the junction of crown and root there is on the inner face of the crown a ledge, shelf or heel. The inner face of this shelf looks like a cingulum lying obliquely with the outer part situated higher than the inner. This inner face is convex and on the occlusal face presents a rounded edge lying behind the half-moon-shaped depression lying between it and the inner face of the talon.

The roughly conical cusp lying below the heel is here referred to as the talon. The inner face of the talon is flattened with a low median and lateral ridges.

Canines

The canine is a large, somewhat recurved conical tooth, slightly laterally compressed so that its section is oval. The length of the crown is 110 mm. and at its base the diameters are 45×30 mm. From about half-way down the crown its postero-external face forms a fairly sharp edge but without any trace of serrations. It thus appears to be a remnant of a truly cutting edge.

Postcanines

The postcanines follow close on the canine without any real diastema. A series of thirteen teeth is preserved of which the first twelve occupy a length of 118 mm. They decrease in size from front to back. The first postcanine has the crown imperfectly preserved; it is directed anteriorly, whereas the others incline posteriorly; it is the largest postcanine and its greater diameter at its base is 12 mm. as against the 8 mm. of No. 2.

The postcanines all have the same general build, viz. a quite long stem oval in section, then a neck followed by a swollen spatulate crown triangular in outline. The crowns lie obliquely to the long axis of the skull, with the anterior edge lying lingually and the posterior edge labially. The outer face of the spatulate crown is convex with longitudinal striae and sharp, somewhat everted external as well as internal edges which are serrate when unworn. The inner face is flattened to concave.

No. 6 has fallen out, but lingually there lies the erupted crown of its

replacing tooth with a flattish crown and serrated edges. No. 11 has its outer face coarsely striate and the edge serrate.

Comparison of the Titanosuchian Dentition with that of the Other Dinocephalian Infra-orders

Earlier in this paper I have stressed a distinctive character common to all the infra-orders of the Dinocephalia and mentioned certain striking features in the dentition peculiar to each infra-order. A more detailed consideration is, however, called for.

ANTEOSAURIA

In the mature anteosaurian skull the dental formula is i $\frac{5}{4}$, c $\frac{1}{1}$, pc $\frac{8}{7}$. The postcanine series thus has a small number of teeth.

Incisors

The incisors are long recurved conical teeth, the greatest length encountered being 100 mm. The housing of these greatly lengthened teeth is made possible by a retreat of the premaxillary alveolar border. Although most incisors studied have a simple conical form with an oval cross-section, there is in the South African forms a faint indication in some teeth of a differentiation of a talon and a slight heel, which is apparently more pronounced in some Russian forms. A fact which would strengthen our argument for close consanguinity with the other dinocephalians.

The intermeshing of the incisors is similar to that of the titanosuchians, but the fifth upper incisor is an antagonist of the lower canine by passing labially to it in occlusion and not anteriorly and does thus not intermesh with it. The replacement of the incisors in the Anteosauria has not been adequately studied, but in a series of five frontal sections which I have cut in one specimen (fig. 33) it is evident that the replacing incisor arises lingually of the functioning tooth as it does in the Titanosuchia. The manner of eruption, however, shows certain differences. The development of pockets in the lingual face of the alveolar wall of the functioning incisors for the emergence of the replacing incisors, which is so typical in the premaxillaries of the Titanosuchia, has not been found in the Anteosauria.

In fig. 33 the five sections show:

Sections 1 and 2: The former section passes just below the alveolar border and the latter just above. On the right side the roots of Nos. 2, 3 and 4 are those of functioning incisors. On the left the functioning incisors Nos. 2, 3, 4 and 5 are seen and lingual of No. 5 lies a section cut through the tip of the lower canine.

Section 3: On both sides the young developing crowns of pair No. 1 appear and on the left the remains of the root of an older member of the family of No. 2 incisor is seen as an as yet unresorbed remnant.

Section 4: The developing right No. 5 incisor can now be seen.

Section 5: The replacing tooth of the as yet unerupted right No. 1 incisor is already commencing its development, i.e. before the other older incisors develop any replacements.

Canines

The upper canines are large slightly recurved pointed teeth with crowns up to 120 mm. in height, flattened from side to side with a sharp posterior edge in which no serrations have been seen. The lower canines are not directed outwards to pass in between the upper fifth incisor and the upper canine as they

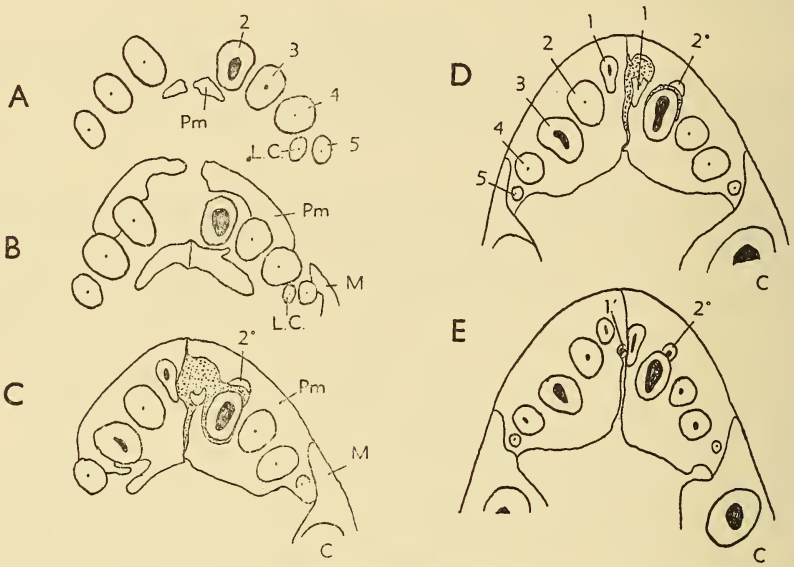


Fig. 33. *Anteosaurus abeli.* S.A.M. 9123. ×¼.
Five consecutive frontal sections through the snout showing the replacement of the incisors.

do in the Titanosuchia, but are directed upwards and have their tips received in a hollow in the maxillary surface anterior to the base of the upper canine.

Practically nothing is known of the replacement of the canines, but in one specimen an upper canine appears to have its crown about to be shed and lying posterior to it is a pointed tooth which may be its replacement. If this observation be correct then the replacement of the anteosaurian canine would be different from that of the Titanosuchia and be similar to that known in the contemporary Therocephalia and Gorgonopsia.

Postcanines

In the Anteosauria the postcanines are inadequately known. They form a short series with at most 8 teeth, irregularly spaced. The crowns are spatulate, bluntly conical in outline and bulbously swollen from side to side.

TAPINOCEPHALIA

The dentition of the South African Tapinocephalia is as yet inadequately known (fig. 34). This is mainly due to the fact that in most of the jaws known the teeth have been lost before entombment, and in many cases where they have been petrified while still in the jaws they have on subsequent erosion dropped out or have had the crowns broken off or otherwise damaged.

As the Tapinocephalia have in neither upper or lower jaw teeth specialized as canines, the usual connotation cannot be employed. The teeth in the premaxilla will be referred to as incisors and the others as maxillary and dentary teeth. A dental formula on this basis for the Tapinocephalia would thus read:

$$\frac{\text{Premaxilla } 3\text{–}5,\ \text{Maxilla } 8\text{–}17}{\text{Dentary } 14\text{–}19}$$

Whether the differences in the count given here have much taxonomic value is to be doubted, and in absence of the necessary facts I am more inclined to suggest inadequate observation coupled with the probability that age is an important factor. It is more than probable that the incisor count of 3–5 may, as is the case in the Anteosauria, only signify a difference in age, with 5 incisors the count for the mature animal.

All the teeth of the mature upper jaw intermesh with those of the mandible, but this intermeshing becomes gradually less definite posteriorly.

All the more anteriorly situated teeth when mature have the same general build, with the crown consisting of a piercing pointed cusp or talon and lingually a cutting and/or crushing heel in general similar to those of the incisors of the Titanosuchia. As will be evident from figure 34 the anterior or incisor teeth of the Tapinocephalia differ, however, in detail from those of the Titanosuchia. Some of the differences in the incisors are here enumerated:

(1) The roots are laterally compressed and the linguo-labial diameter greatly increased thus giving a very flat oval cross-section (diameters 24–40 by 13–19 mm.);

(2) the crowns are similarly laterally compressed and the linguo-labial diameter over the heel greatly increased (diameters 31–43 by 16–20 mm.);

(3) the talons are much shorter; in the Titanosuchia the crown is about the same length as the root, whereas in the tapinocephalian incisors it is about five-eighths;

(4) the nature of the heel shows considerable differences; in the Tapinocephalia the occlusial face of the heel presents a fairly deep oval hollow bounded labially by the talon, anteriorly and posteriorly by a sharp edge with a slight spur lingually. The anterior (or inner) edge lies much higher than the posterior (or outer) edge.

Further back in the series the tapinocephalian teeth gradually lose these incisor characters and begin to look more like titanosuchian incisors, except that the talons remain short. The labio-lingual diameter gradually decreases

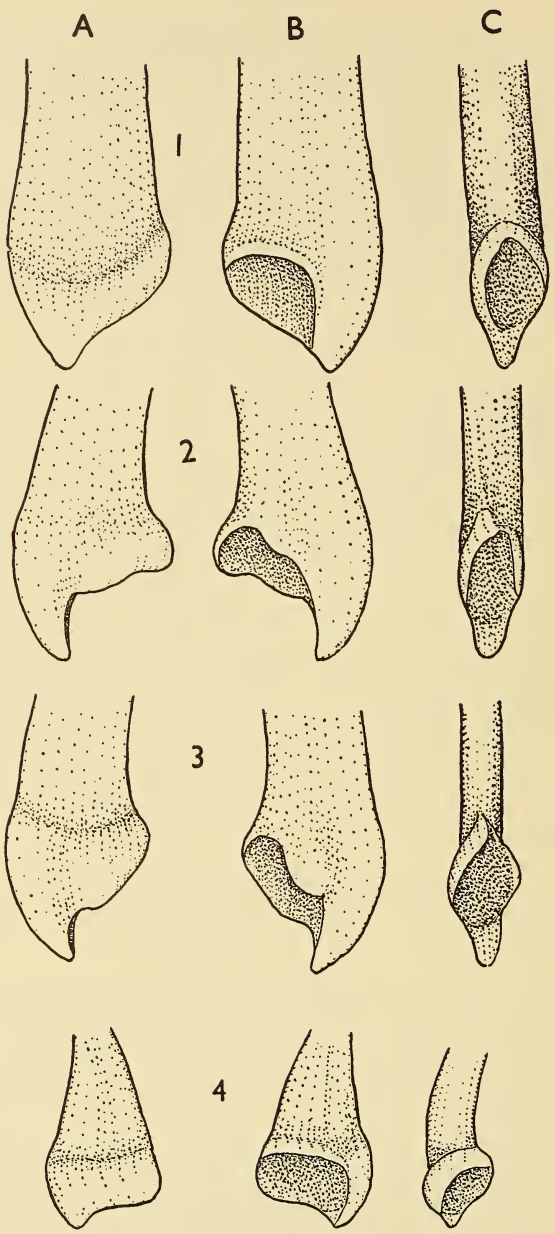


FIG. 34. *Tapinocephalus*. S.A.M. K203. $\times \frac{1}{2}$.
Four anterior teeth of the right upper jaw shown:

A = anterior (or inner) view.
B = posterior (or outer) view.
C = lingual view.

in length, the sharp ridges on the heel become lower, the face of the heel loses its concavity and even develops a median ridge. Still further posteriorly the linguo-labial character becomes still less and the lingual edge of the heel begins to look very titanosuchian-like, although much smaller in size.

Near the posterior end of the series the teeth lose the heel altogether and the crown becomes spatulate and looks very like those of the postcanines of the Titanosuchia (fig. 35).

We may summarize the above observations as follows:

In a series of functional teeth in the tapinocephalian jaw the posterior teeth have spatulate crowns, which, as one proceeds anteriorly, step by step

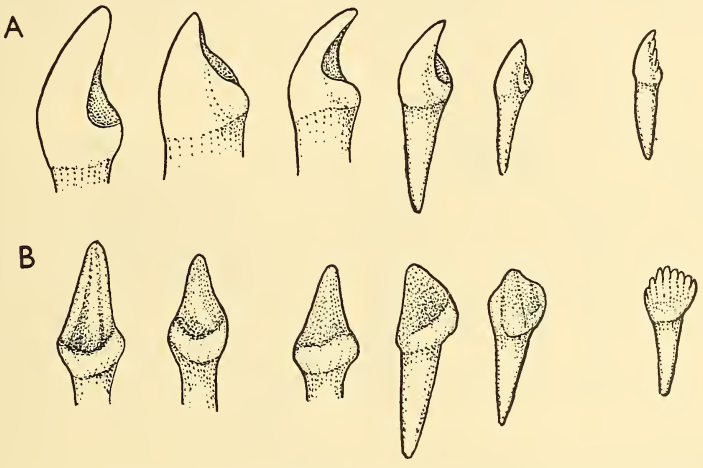


FIG. 35. *Struthiocephalus whaitsi*. S.A.M. 3012. $\times\frac{1}{2}$.
Six right upper teeth lying loose under a skull from which they have dropped.
A = posterior (or outer) view. B = lingual view.

develop a pointed talon and a heel, the heel commencing as a lingual thickening, becomes, firstly, a cingulum, then a step; this step develops a bounding edge with a face between it and the talon; the edge becomes sharper and the face hollower and this hollow increases its linguo-labial diameter.

In one genus (*Agnosaurus*) evidence is preserved that a set of unerupted small spatulate teeth is being replaced by a younger set, which has crowns composed of a talon and heel. This replacement commences anteriorly and proceeds posteriorly, but is not evident anterior to the 6th or 5th tooth in the dentary.

Tapinocephalus sp.

S.A.M. 12139. Rietfontein, P.A. Collected Boonstra 1957.

In a weathered skull of *Tapinocephalus* (fig. 36), where only roots and empty alveoli are preserved, some features of the replacement of the teeth are shown.

In the left premaxilla the roots of five functioning incisors are preserved. Lingual to No. 5 there is a large replacing root lying in the same alveolus as the functioning root which has been partly resorbed. In No. 4 a functioning root lies loosely in its alveolus and lingual to it in a separate alveolus, a section across the replacing root is present. Lingual of No. 3 there is an empty alveolus and lingual of No. 2 there lies a root of its replacing incisor.

In the right maxilla replacing roots are preserved lying lingual to maxillary teeth Nos. 2 and 10. In the left maxilla the roots of the first two maxillary teeth are seen in section; Nos. 3 and 4 are represented by a large confluent alveolus; of No. 5 the small tip of a root is embedded in the bone. No. 6 is represented by an empty alveolus. No. 7 is again a root-tip embedded in the bone. No. 8 is represented by a small root-tip lying loosely in an alveolus confluent with the

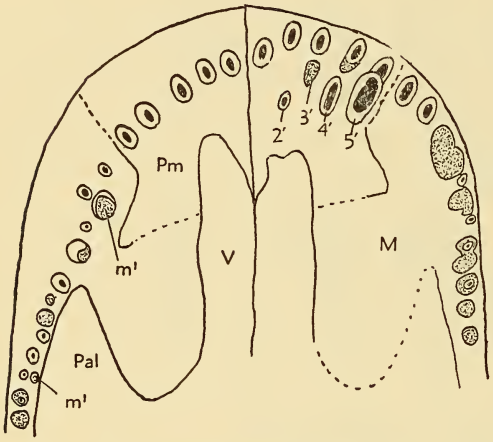


Fig. 36. *Tapinocephalus* sp. S.A.M. 12139. ×¼.
Ventral view of the anterior part of the palate showing tooth replacement.

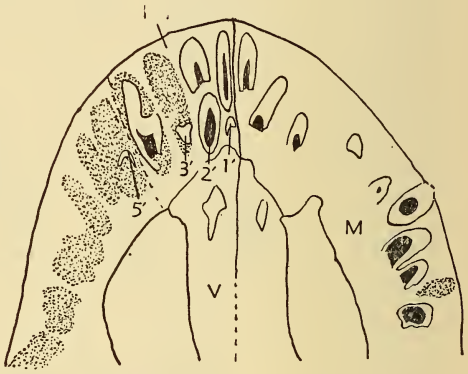


Fig. 38. *Struthiocephalus* sp. S.A.M. 12050. ×¼.
A frontal section through the anterior end of the upper jaws to show the tooth replacement.

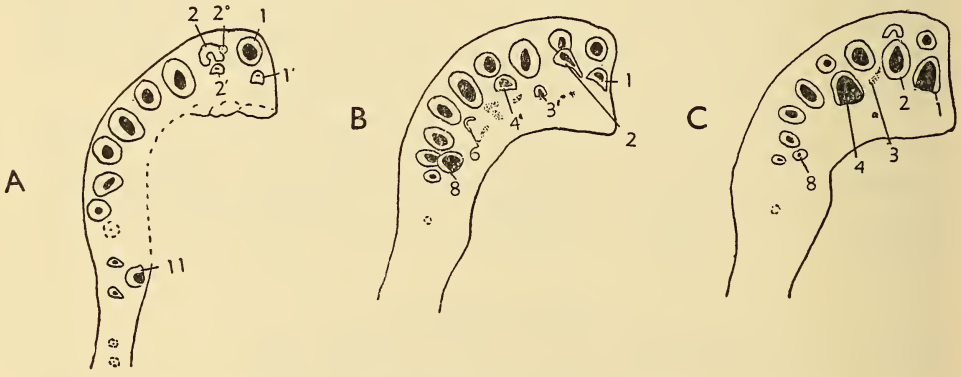


Fig. 37. *Tapinocephalus* sp. S.A.M. 12139. ×¼.
Three frontal sections through the left dentary showing tooth replacement.

empty alveolus of No. 9. No. 10 is again a small root-tip lying loosely in the alveolus. Nos. 11 and 12 are represented by empty alveoli.

I have cut three frontal sections through the anterior end of the left dentary to determine the nature of the replacement (fig. 37).

Section 1. The 2nd functioning tooth shows a root being resorbed, with the remnant of a still earlier root lying antero-internally. And lingual to both Nos. 1 and 2 lie sections through the talons of their replacing teeth. Lingually of Nos. 10 and 12 is the tip of the talon of the replacement of No. 11.

Section 2 shows replacements of Nos. 1, 2, 3, 4, 6 and 8 and an empty cavity lingual to No. 5. Further lingually, cavities for a second set of replacements are seen for Nos. 2, 4, 5 and 6.

Section 3 shows replacements of Nos. 1, 2, 4 and 8 and a cavity for No. 3 first replacement and a cavity for No. 3 second replacement.

Struthiocephalus sp.

S.A.M. 12050. Modderfontein, Laingsburg. Collected Boonstra 1957.

I have cut some frontal sections through the snout of a good skull of *Struthiocephalus*, but as most of the teeth have been lost before petrifaction the evidence obtained of the replacement of the teeth is poor (fig. 38).

In the right premaxilla can be seen: a narrow root of No. 1 with lingually to it the tip of the talon of its replacement.

No. 2 shows the partially resorbed root of the functioning tooth with lingual to it a well-developed replacement.

Of No. 3 there is a large oval alveolus from which the functioning tooth has dropped out, and in its lingual end lies the tip of the replacing talon.

No. 4 shows a well-developed, but as yet unerupted, crown with talon and heel.

In the maxilla large irregular alveoli can indistinctly be seen with a section through a replacing talon lying loosely in the first maxillary alveolus.

In the right half of the upper jaw there is evidence of twelve teeth of which Nos. 1, 8, 9, 10 and 12 were functioning, No. 11 is represented by an empty alveolus and Nos. 3, 4, 6 and 7 are represented by replacing teeth. On this scanty evidence we may tentatively state that the replacement in the Tapinocephalia takes place lingually of the functioning teeth as it also does in the Titanosuchia and the Anteosauria. The anterior (incisor) teeth do not emerge through pockets in the alveolar walls of the functioning teeth as they do so typically in the Titanosuchia. In this they agree with the condition, also tentatively, seen in the Anteosauria.

Comparison with the Contemporary Therapsids

The relevant comparative facts are known in a number of the contemporary Therocephalia and Gorgonopsia of the *Tapinocephalus* zone.

In these older therapsids there are usually more (1–2) incisors, but the number of postcanines is always much smaller than in the Dinocephalia. Primitively there were two functional upper canines, but in most the upper canines have been reduced to one only. All the teeth are simple, conical but with serrations developed, usually on the posterior edge, in the incisors and canines.

The dentition in these two sub-orders was thus carnivorous.

As in the Dinocephalia each tooth is replaced lingually by a member of its own family and this replacement occurs more than once.

In the Dinocephalia there is a single alveolus for the upper canine, whereas in these Therocephalia and Gorgonopsia there are two alveoli. Primitively these two alveoli house functional canines at the same time, but in the other forms the functional canine appears alternately in the two alveoli.

PELYCOSAURIA

In the older and more primitive Pelycosauria there may be as many as 9 incisors and up to 45 maxillary teeth. In the later Sphenacodontia a pair of teeth becomes functional canines.

All the teeth are simple, conical, but sometimes become serrate.

Each tooth is replaced lingually by a member of its own family.

Primitively the functional replacement of a tooth is by the replacing member of an adjacent tooth—thus distichially, but in the more advanced Sphenacodontia the functional replacement is by a member of its own family, except in the case of the upper canines which are replaced alternately.

The Origin and Further Development of the Dinocephalian Dentition

The story of the origin and further development of the dinocephalian dentition starts from some such point as seen in the less specialized Pelycosauria.

Both upper and lower jaws have a large number of teeth—all being simple conical structures, with the upper set, in occlusion, passing labially of the lower set. The dentition is of an unspecialized 'carnivorous' nature.

Each functioning tooth is during life replaced a number of times by a tooth, which arises lingually to it, but as each functioning tooth is lost its function is not immediately taken over by the tooth arising lingually to it but this function is assumed by the tooth arising in the adjacent alveolus (distichial replacement).

This simple type of dentition is changed, when in the maxilla two of the more anterior maxillary teeth become larger than the rest and are then called 'canines'. Not much later a further change takes place, when each of the teeth, not canines, is functionally as well as actually replaced by the tooth arising in the jaw lingually to it. The pair of canines is replaced alternately, i.e. when

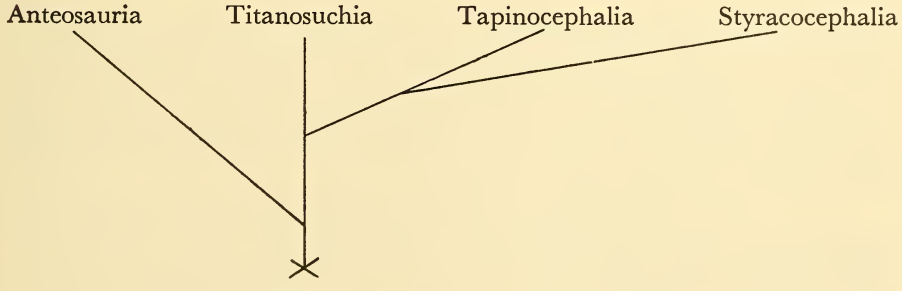
both are not functioning at the same time either the anterior or the posterior one assumes the function of both. This is the stage reached by the Sphenacodontia.

The next stage is one to be postulated for the ancestral therapsid or pro-therapsid. Here the dentition would consist of about 7 upper incisors, a pair of canines, which are the first two teeth on the maxilla, numerous postcanines; one incisor less in the dentary, a single lower canine and a long row of postcanines. All the teeth would be simple conical teeth, with probably serrated edges in the incisors and canines.

From some such pro-therapsid stage the various primitive therapsid sub-orders diverged. One of these branches represents the sub-order Dinocephalia. In the ancestral dinocephalian the dentition must have been as follows: 5 upper and 4 lower incisors, a single upper and lower canine and numerous postcanines. All the teeth were still simple conical structures with or without serrated edges. Each functioning tooth was replaced by a tooth arising lingually to it. In occlusion all the teeth of the upper jaw passed labially of the teeth of the lower jaw and the dentition was definitely of a habit usually interpreted as being 'carnivorous'. In the next stage, this carnivorous dentition with upper teeth occluding labially of the lower teeth, changed to a carnivorous dentition in which the incisor teeth commenced to intermesh with each other.

This development of intermeshing incisors was a step which definitely split the Dinocephalia off from the other Therapsida and set them off on their own separate course, and it is the possession of this distinctive character that we consider to be a major justification of our considering the Dinocephalia to constitute a distinct sub-order.

Although continuing to retain this common character the Dinocephalia very soon started to develop divergent features. The first dichotomy appears to have split off the infra-order Anteosauria from the rest; from the latter branch a further dichotomy split off the Titanosuchia and still later the Tapinocephalia and Styracocephalia developed as two divergent branches.



ANTEOSAURIA

In the nature of its dentition the Anteosauria appear to have changed least from the above postulated condition.

The incisors have retained the simple conical structure, the canines are retained and the postcanines are still simple teeth.

But certain specializations have taken place, viz. the original fairly small incisors have become greatly elongated, and this increase in length is made possible by a concomitant upward retreat of the premaxillary edge; the canines have greatly increased in size and provision for the reception of the tip of the lower canine is made by the development of a recess in the lower face of the maxilla antero-internally of the base of the upper canine; the postcanines have been reduced in number (maximum of 8) and the simple pointed crown has become spatulate with a bulbous outer face.

These specializations have changed the original simple carnivores into anteosaurs, with a highly efficient grab, pierce-and-tear dental instrument. With a slinking habit (deduced from the structure of the limbs) such a dentition would allow of a sudden pounce on its prey, and the tearing out of a lump of flesh. The degeneration of the postcanines indicates that no shearing, cutting or grinding took place prior to the deglutition of the lump of flesh helped by the teeth on the palatine boss.

TITANOSUCHIA

In the Titanosuchia the development away from the ancestral condition was much greater and this can be described as follows: The incisors have completely lost their original simple pointed form and have become highly specialized piercing, cutting and crushing teeth. The strong point, cusp or talon situated labially is a highly efficient piercing instrument and it is held very firmly in the jaw by a large strong root. The well-developed heel situated lingually on the crown has a structure adapting it very well for cutting and crushing. Although such incisors could execute a bite into flesh of no mean order they can hardly be considered to be efficient piercing and cutting instruments adapted for biting into flesh and the crushing abilities of the heel would serve no reasonable purpose when applied to meat. For piercing, cutting and crushing hard fibrous vegetable tissue these teeth would be highly efficient and well adapted.

The large canines can reasonably be considered a relict of former carnivorous days, retained and even enlarged to be employed complementary to the incisors for piercing and severing fibrous material. This is most probably the reason why the lower canines have changed their direction to become teeth intermeshing between the last upper incisor and the upper canine and thus really forming part of the incisor-battery.

The postcanines have not been reduced in number and may even have been increased and their serrate spatulate crowns forming a low row along the margins of both jaws could very well have been of use in vegetable feeding.

TAPINOCEPHALIA

In the Tapinocephalia the development away from the ancestral condition has been greater than in both the Anteosauria and the Titanosuchia.

In the former only the incisors intermesh and in the latter the canines are, as a further step, included in this intermeshing, and now as a third step the Tapinocephalia have the maxillary set of teeth intermeshing with the posterior dentary teeth, with a concomitant loss of the specialized canines. The inclusion of the maxillary teeth in this intermeshing commences anteriorly and then gradually extends to the end of the tooth rows. This process includes the change from spatulate teeth to teeth in which a talon and heel is developed. It has been indicated how the change from spatulate teeth to talon-and-heel teeth has taken place in the maxillary and posterior dentary teeth, but in no specimen have we seen any indication that premaxillary and anterior dentary teeth (incisors) were once spatulate and then became tooth-and-heel teeth. Though in some Russian anteosaurs Orlov (1959) found that the conical incisors develop an attrition face that may be the beginning of a heel.

The point now seems to be whether from a simple conical ancestral incisor the Titanosuchia and the Tapinocephalia developed talon-and-heel incisors independently or whether it was the Titanosuchia who took this step and handed the condition on to the Tapinocephalia. If the latter alternative is accepted, then it must be maintained that more or less at the same time, the large titanosuchian canines also became talon-and-heel teeth fitting nicely into the tapinocephalian series. We have noticed the development of attritional faces in the titanosuchian canines which can be interpreted as indicating such a development of talon-and-heel teeth.

Certain differences in the structure of the incisors of respectively Titanosuchia and Tapinocephalia have already been pointed out. Now, do these differences indicate that talon-and-heel teeth have been developed on two separate occasions independently of each other, or do the similarities rather point to a common origin?

The tapinocephalian incisor can be readily derived from the titanosuchian incisor. If in the titanosuchian incisor the length of the talon is reduced, the labio-lingual diameter of the heel increased and the inner edge of the heel raised to form a high and sharp cutting edge then we have a tapinocephalian incisor.

If such a development took place it could have been caused by a change in the nature of the vegetable food. The reduction of the size of the talon of the incisor together with the loss of the specialized canines could be due to the food becoming less hardy and fibrous and thus not necessitating piercing, prising and tearing off. The improved cutting abilities of the heel would at the same time be a better adaptation for the cutting of leafy vegetation.

I am thus of the opinion that the tapinocephalian dentition is a development of that present in the Titanosuchia and that the Tapinocephalia hived off from the Titanosuchia after these had acquired the typical talon and heel incisors.

I have based the above account mainly on the South African material, but hope to correlate with the Russian material in the near future.

The Articulation and Movements of the Lower Jaw

(Figs. 39–41)

The quadrate has on its ventral surface a pair of convex condyles separated by a groove and these fit fairly accurately into two concavities separated by a ridge on the postero-dorsal face of the articular. The quadrate is firmly fixed in the skull, being firmly clasped by the squamosal, braced by the quadrato-

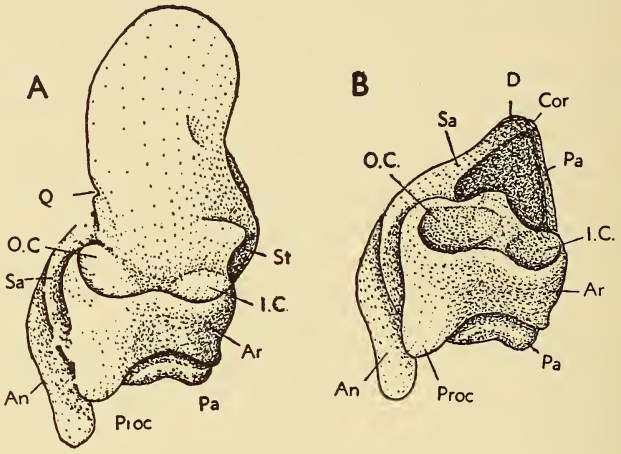


Fig. 40. *Jonkeria truculenta*. S.A.M. 12030. ×¼.
A = posterior view of the jaw articulation.
B = posterior view of the lower jaw.

jugal, butted against by the paroccipital and held by the quadrate ramus of the pterygoid.

The articular is also firmly wedged in between the angular and surangular and the prearticular.

The only possible movement is thus at the joint between quadrate and articular.

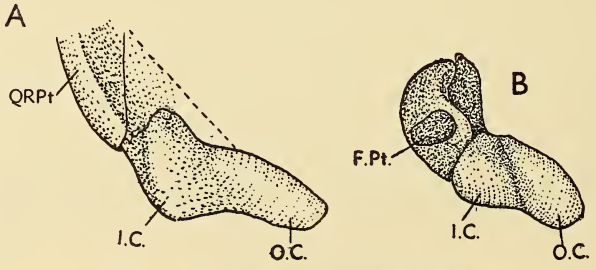


Fig. 39. Ventral view of the quadrate. ×¼.
A = *Parascapanodon avifontis* S.A.M. 9127.
B = *Parascapanodon* sp. S.A.M. 12026.

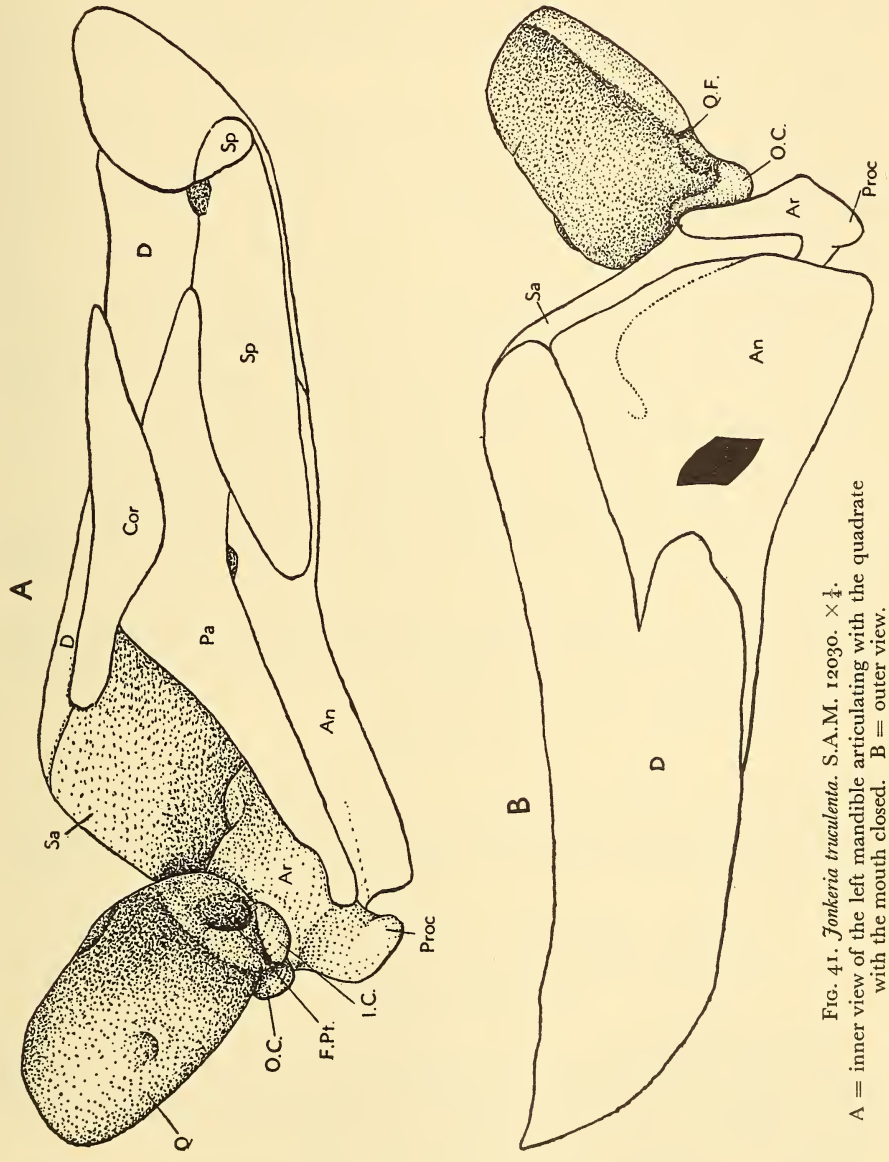


FIG. 41. *Jonkeria truculenta*. S.A.M. 12030. $\times \frac{1}{4}$.
A = inner view of the left mandible articulating with the quadrate with the mouth closed. B = outer view.

The two condyles on the quadrate do not lie in the same plane—the outer lying posterior to the inner. In section they present segments of circles with radii of (in S.A.M. 12026) 26 and 32 mm. which are thus not co-centric. The radii lie in a plane diverging from the sagittal plane in posterior direction. The result of this structure is that when the jaws are opened the movement of the jaws is a sliding one in posterior direction of at least 15 mm. and the backs of both jaws at the same time move outwards for at least the same distance. At the same time the lower edge of the jaw appears to move inwards. The latter two movements are rendered possible by the fact that the two rami of the jaws are not firmly fixed to each other at the symphysis.

What effects do these movements of the jaws have on the bite of a titanosuchian?

The forward movement of the jaws when the mouth is closed would push the talons of the lower incisors from behind forwards between those of the upper incisors and the heels of the lower incisors would slide under those of the upper teeth thus executing a crushing and cutting action. The upper and lower canines would move relatively as do the talons of the incisors, and the lower postcanines would have a cutting action when moving past their upper antagonists.

When the jaws are closed the articulars move towards each other with the result that the more posterior postcanines also move inwards and would thus pass inwards of the upper postcanines leaving some space between the upper and lower teeth.

If the lower mandibular edge, when the jaw is closed, moves outwards, the alveolar edge would move inwards and this would still further increase the space between upper and lower postcanines.

This would be functionally disadvantageous!

Faunistic

Hitherto the main elements of the fauna of the *Tapinocephalus* zone were divided into two groups representing the opposing herbivores and carnivores as follows:

herbivores: Pareiasauria, Tapinocephalia and Anomodontia.
carnivores: Titanosuchia (including the Anteosauria), Therocephalia and Gorgonopsia.

This presumed balance always appeared to be loaded in favour of the carnivores, for not only were the Titanosuchia known to be large reptiles but were in addition numerous, as judged by the frequency in which remains (mostly poor, it is true) are encountered in the field.

In the new picture the herbivores are (and this is more natural) better represented, the largest forms of the times being the herbivores. In order of size the herbivores of this zone are: Titanosuchia, Pareiasauria, Tapinocephalia and Anomodontia, and the carnivores: Anteosauria, Therocephalia and Gorgonopsia.

The more marsh-dwelling herbivores were the Pareiasauria and the Tapinocephalia; the more upland-dwelling forms the Titanosuchia and Anomodontia. Of the carnivores the Anteosauria, with large heads, were more of a slinking habit; the Therocephalia more active upland reptiles of prey, and the Gorgonopsia just starting their role as important carnivores.

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In the collection of the material here described I am pleased to be able to express my gratitude to all those farmers in the Karoo who have so kindly allowed me to work on their property, helped me in various ways, and always been most hospitable. Mr. H. Zinn, technical assistant of the Museum, has accompanied me on many of the collecting trips and has been most helpful.

In recent years C.S.I.R. has given me a grant which covered the current expenses of the collecting trips undertaken.

Mr. C. Gow has during the last year assisted in the preparation of many of the jaws studied. His painstaking work, chiefly with a vibro-tool, has produced some really adequately prepared specimens.

The sections made of a number of specimens were rendered possible by the use of a diamond-studded rotating saw purchased with a grant made by C.S.I.R.

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